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The Noronha Vireo *Vireo gracilirostris* (top) compared with its closest relative and probable direct ancestor *Vireo olivaceus chivi* (bottom) of the Red-eyed Vireo complex. Painting by William Zimmerman.

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THE ENDEMIC VIREO OF FERNANDO DE NORONHA (*VIREO GRACILIROSTRIS*)

STORRS L. OLSON[1]

ABSTRACT.—The Noronha Vireo (*Vireo gracilirostris*) is endemic to the small oceanic island of Fernando de Noronha off the easternmost tip of Brazil. Although derived from the Red-eyed Vireo (*V. olivaceus*) complex, the Noronha Vireo is differentiated strongly in coloration, plumage pattern, and morphology and fully merits recognition as a distinct species. It is a smaller bird with a much more rounded wing, longer, more slender bill and a more elongated tail and tarsus. These appear to be specializations for gleaning small insects from foliage, particularly the undersides of leaves. The birds are abundant where appropriate habitat is maintained. The few available data on reproductive and molt cycles, nesting, and vocalizations in *V. gracilirostris* are summarized.

Received 11 November 1992, accepted 24 March 1993.

The archipelago of Fernando de Noronha is the easternmost extension of land in the Neotropics, lying 345 km east of the eastern tip of mainland Brazil (3°50′S, 32°25′W). It consists of one main island with a string of minor rocks and islets at its northeastern end and various other scattered stacks. The total land area is 18.4 km^2. The island is volcanic in origin and before its discovery in 1503 probably was almost entirely forested. The avifauna consists of the usual complement of tropical seabirds, an as yet undescribed extinct flightless rail (Olson 1982), the Eared Dove (*Zenaida auriculata*), and the easternmost populations in the world of tyrant flycatcher (Tyrannidae) and vireo (Vireonidae). The flycatcher generally is considered to be an endemic subspecies of the Large Elaenia (*Elaenia spectabilis ridleyana*) (Traylor 1979), whereas the Noronha Vireo is a highly distinctive endemic species, *Vireo gracilirostris*.

Little has been written about *V. gracilirostris*, and apart from a sketch of the bill (Sharpe 1890:478), a black-and-white photograph of a live bird

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(Nacinovic and Teixeira 1989), and photographs of the skull and sternum (Barlow and Bortolotti 1989), the species has not otherwise been illustrated. I here bring together the scattered literature on this species, my own observations made on the island nearly 20 years ago, and further illustrative material.

HISTORY OF OBSERVATIONS AND COLLECTING

Opportunities for studying vireos on Fernando de Noronha have been limited (Table 1). The first recorded observation of the species is that of Moseley (1892:68), a naturalist on the *Challenger* Expedition who noted "a small warbler (*Sylvia*), with greenish brown plumage" when the *Challenger* visited the island in 1873. Unfortunately, the expedition was refused permission to conduct investigations on the island, and no specimens were collected.

In 1887, the biology of Fernando de Noronha was investigated comprehensively for the Royal Society by H. N. Ridley (1890a, b). Five specimens of vireos were taken at this time, upon which Sharpe (1890:478) based the original description of *V. gracilirostris*. Ridley (1888:44) noted only that the vireo was common and "frequents the cashew-nut tree and the cocoa-nut palms. It is a small green bird, like a Willow Wren [*Phylloscopus trochilus*], very active, but by no means difficult to shoot. We never succeeded in finding its nest."

The species was next encountered by Nicoll (1904:38, 1908:16), who was on the island in 1903. He noted that the species was fairly abundant, and he likened it to a Eurasian Reed Warbler (*Acrocephalus scirpaceus*) in its actions. On 15 October 1912, Murphy (1915:50) encountered "many of these greenlets . . . in the fig trees and in the thickets near the beach" and collected a pair in fresh plumage.

The *Blossom* Expedition of the Cleveland Museum of Natural History collected extensively in the South Atlantic from 1923 to 1926. Fernando de Noronha was visited in 1926, when 40 specimens of vireos were obtained, among other species. The expedition was poorly equipped, however, and experienced many difficulties with personnel and provisions. The only publication dealing specifically with the expedition is a popular account by the leader Simmons (1927), and the only scientific information now retrievable is from specimen labels and the field catalog. The bulk of the collection is at the Peabody Museum of Yale Univ., but parts of it have been rather widely dispersed.

There seems to have been no further ornithological exploration of Fernando de Noronha until my sojourn in 1973 (Olson 1982). Oren (1982, 1984) visited the island in 1980 and again in 1982. Nacinovic and Teixeira (1989) record ornithological observations made on three visits to Fernando de Noronha in the 1980s.

SYSTEMATICS AND MORPHOLOGY

Vireo gracilirostris Sharpe

Noronha Vireo

"small warbler (*Sylvia*)" Moseley, 1892:68.

Vireo gracilirostris Sharpe 1890:478 (orig. descr., fig. of bill).—Nicoll, 1904:38.—Nicoll, 1908:16.—Hellmayr, 1935:144.—Pinto, 1944:401.—Santos, 1948:177.—Warren and Harrison, 1971:212.—Olson, 1982:482.—Oren, 1982:13.—Oren, 1984:36.—Sick, 1984:644.—Nacinovic and Teixeira, 1989:723 (photograph of live bird).—Barlow and Bortolotti, 1989:1536–1537, 1540–1545 (skull and sternum figured), 1547.—Ridgely and Tudor, 1989:150.

TABLE 1
SOURCES OF OBSERVATIONS AND SPECIMENS OF *VIREO GRACILIROSTRIS* AT FERNANDO DE NORONHA

Expedition	Duration	N[1]	References
Challenger	1–2 Sept. 1873	0	Moseley 1892
Royal Society	14 Aug.–24 Sept. 1887	5	Ridley 1888, 1890a, b
Valhalla	20–25 Dec. 1903	5	Nicoll 1904, 1908
Daisy	15 Oct. 1912	2	Murphy 1915
Blossom	18 March–26 April 1926	40	Simmons 1927
Smithsonian	6 July–18 Aug. 1973	22	Olson 1982
Museu Goeldi	16 Nov. 1980 1–13 Dec. 1982	17	Oren 1982, 1984
Museu Nacional	25 Sept.–1 Oct. 1983 8–22 June 1986 25–30 Sept. 1988	7	Nacinovic and Teixeira 1989

[1] N = number collected.

Vireosylva gracilirostris.—Murphy, 1915:50.—Murphy, 1936:148.
Vireo olivaceus gracilirostris.—Meyer de Schauensee, 1966:424.—Mayr and Short, 1970: 72.—Orenstein and Barlow, 1981:4, 20, 32.

Local people on the island call the vireo "*sibito.*" Although Oren (1984) spelled the name "*sebito,*" Nacinovic and Teixeira (1989) use "*sibito,*" which is the spelling I was given. This name, according to Oren (1984), is used in northeastern Brazil for various nondescript birds.

As the preceding synonymy shows, the Noronha Vireo has almost always been treated as a distinct species. In his original description, Sharpe (1890) ventured that "there is no doubt that the Fernando Noronha bird comes nearest to *V. magister,*" a conclusion repeated by Sick (1984), probably on Sharpe's authority only. *Vireo magister* is a vicariant form of the Black-whiskered Vireo (*V. altiloquus*) that occurs in Yucatan, Belize, and Grand Cayman.

In discussing *V. gracilirostris,* which they considered to stand "apart on so many counts that it amply deserves recognition as a full species," Ridgely and Tudor (1989:150) stated erroneously that "since Hellmayr [1935] this form has been considered merely an insular race of *V. olivaceus.*" Although Hellmayr synonymized species on many occasions, this was not one of them, the deed apparently having been done first by Meyer de Schauensee (1966) but merely in a compilation with no systematic revisionary study.

What Hellmayr (1935:144, footnote) actually said is still pertinent today:

> "This peculiar species is quite distinct from the continental *V. virescens* [=*olivaceus*] *chivi,* from which it differs, in addition to coloration, by proportionately much longer tail, very much slenderer as well as longer bill, and shorter first primary, the latter being either equal to, or a little longer than, the seventh. In general coloration it is indeed not unlike *V. magister,* though it may be readily distinguished from it by much shorter wings, slenderer tarsi, much smaller and slenderer bill, the absence of the dusky loral spot and the grayish suffusion on the sides of the body, etc. I cannot believe that any genetic relationship really exists between these birds. . . ."

Plumage.—The subdued coloration and slender proportions of *V. gracilirostris* give it a strong superficial resemblance to an Old World warbler (Sylviidae), as noted by several early naturalists. The species has been described in some detail by Sharpe (1890) and Hellmayr (1935), and additional specimen measurements are found in Oren (1982) and Nacinovic and Teixeira (1989). I will therefore confine my remarks to direct comparisons with its presumed closest relative, *V. olivaceus chivi* (I use the term here in a collective sense to mean all of the South American populations of the complex, exclusive of *V. flavoviridis*).

Compared to *V. o. chivi* (Frontispiece), the dorsum of the Noronha Vireo is brownish anteriorly rather than green, and the gray cap is lacking, so that the crown is essentially the same color as the back. Most specimens in North American collections are from the indifferently prepared, and exceedingly worn and faded, series taken by the *Blossom* expedition. These give the appearance of a very brownish or grayish bird, whereas in fresh plumage the lower back, rump, and margins of the flight feathers are decidedly green. There is some individual variation, as one specimen in the series I obtained is much grayer above, with little brown or green in the plumage.

The black dorsal border of the superciliary stripe of *V. o. chivi* is lacking in *V. gracilirostris,* the superciliary itself is less pronounced and buffy rather than whitish, and the dark preocular spot is brownish rather than blackish. The underparts of *V. gracilirostris* are washed with buff, palest on the lower belly but not white with greenish flanks as in *V. o. chivi.* The underwing and under tail coverts are yellow in *V. o. chivi* but buffy in *V. gracilirostris,* although the crissum is yellowish buff in some individuals.

One specimen that I obtained is still mainly in the lax, fluffy juvenile plumage, with the crown, back, and secondary coverts a rich rusty brown, rather similar to that in the *V. olivaceus* group in general but more reddish than in juveniles of *V. olivaceus* itself.

Soft-part colors.—My annotations indicate that the iris is brown, the

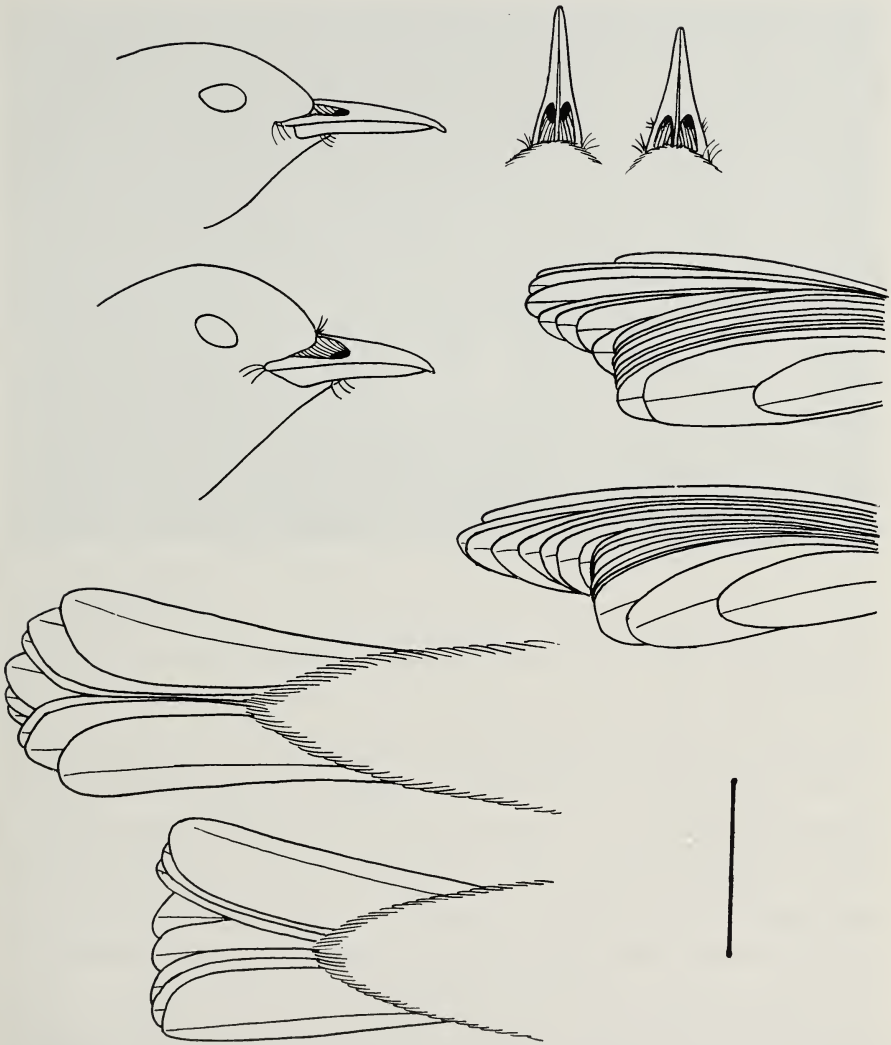


FIG. 1. Comparison of external morphology of *Vireo gracilirostris* (top in each pair, on left in dorsal view of bills) with that of *V. olivaceus chivi* (bottom in each pair, on right in dorsal view of bills) showing bills in lateral and dorsal views, wingtips in dorsal view, and tails in ventral view. Scale = 2 cm.

upper mandible brownish-horn, the lower mandible whitish, and the feet light bluish-gray.

External morphology.—The more obvious distinctions of *V. gracilirostris* in external morphology and proportions are shown in Figs. 1 and 3 and Table 2. The longer and obviously more slender bill (both in width

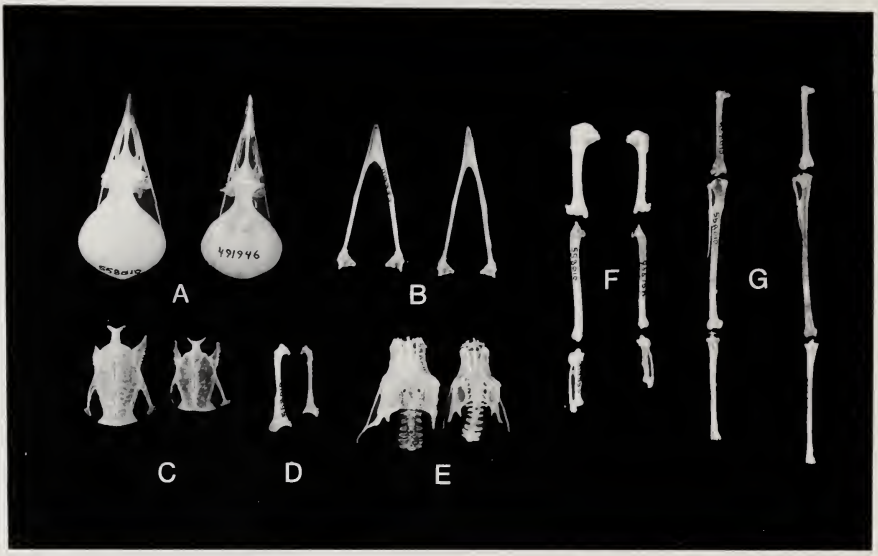


FIG. 2. Comparison of skeletal elements of *Vireo olivaceus chivi* (USNM 558010—on the left in each pair) with *V. gracilirostris* (USNM 491946—on the right in each pair). A, skulls in dorsal view; B, mandibles in dorsal view; C, sterna in ventral view; D, coracoids in ventral view; E, pelves in dorsal view; F, wing elements; G, leg elements. All figures about ¾ natural size.

and depth) give rise to the specific name, and the tail is much longer than in the *V. chivi* group. As noted above, Hellmayr (1935) remarked on the shorter first primary, to which may be added that the entire wing tip (distance between the tips of the secondaries and tips of the primaries) is shorter (Fig. 1E, F). Despite this and the fact that the pectoral girdle and wing elements are smaller in *V. gracilirostris,* the overall wing size, as indicated by the chord length, does not seem to be as correspondingly reduced, as there is considerable overlap in measurements.

The differences in wing shape are shown in Fig. 3. The wing in *V. gracilirostris* is broad and rounded, whereas in the highly migratory *V. olivaceus* the wing is long and pointed. The differences are exaggerated here by contrasting the most migratory form with perhaps the most sedentary member of the *V. olivaceus* complex. It is likely that *V. gracilirostris* does not differ as much in wing shape from the more sedentary forms of the *V. o. chivi* group. Unfortunately, no spread wings were available for any of these taxa.

By simply tracing the outline of the two specimens shown in Fig. 3 on graph paper, I found that the wing area was identical (27.0 cm^2). This probably indicates that wing area cannot be reduced below a certain

FIG. 3. Comparison of wing shape in *Vireo olivaceus* (left) and *V. gracilirostris* (right). Although the wing shape is quite different in these two species, with that in the highly migratory *V. olivaceus* being very long and pointed, the surface area was identical in these two specimens. Scale = 2 cm.

amount without adversely affecting arboreal foraging, so that *V. gracilirostris* maintains the same wing area while having a much smaller pectoral girdle and associated musculature, which is advantageous in a sedentary, insular species.

Osteology.—Barlow and Bortolotti (1989) compared aspects of the skeleton of *V. gracilirostris* with other members of the *V. olivaceus* complex (but not *V. chivi* or *V. flavoviridis*), among which it was almost always the most divergent and in one principal component analysis (Barlow and Bortolotti 1989: fig 4) was widely separated from the other taxa. Additional data and analyses are provided here in Table 2 and Figs. 2 and 4.

Such standard indicators of overall size as cranium width and femur length show *V. gracilirostris* to be, on average, a slightly smaller bird but with considerable overlap. All elements of the wing and pectoral girdle are much smaller in *V. gracilirostris,* but so too is the pelvis. In plotting the combined lengths of sternum and coracoid versus combined lengths of the wing elements (Fig. 4b), *V. gracilirostris* falls out on the same slope as *V. olivaceus,* which seems to indicate that it is simply a smaller bird, rather than having a disproportionately reduced pectoral girdle. Barlow and Bortolotti (1989) found that relative to the total length of the wing elements, the humerus in *V. gracilirostris* is shorter and the carpometacarpus longer than in related taxa, whereas the ulna remains the same. In absolute measurements the lengths of the tail, culmen, and tarsometatarsus are greater in *V. gracilirostris,* with no overlap. Bill width in the skeleton is consistently smaller, and bill depth in skins is likewise small in *V. gracilirostris,* although with some overlap.

In sum, compared to *V. olivaceus* (including *V. o. chivi*), the Noronha Vireo is a smaller bird with a longer, more slender bill, and much longer

tail and tarsus. The wing is rounded rather than pointed, but retains the same surface area, possibly in part through relative elongation of the carpometacarpus.

Mass.—Unfortunately, I was unable to obtain mass data for the specimens I collected; the only such information comes from Nacinovic and Teixeira (1989), who gave the masses of seven individuals of *V. gracilirostris* as ranging from 11.5 to 20 g (mean 16.5). This seems a rather great disparity for a small non-migratory passerine, particularly as one bird at the low end of the range (12 g) was noted as being very fat. The mean mass of seven individuals of *V. o. chivi* from Peru was 13.8 g, and migratory *V. o. olivaceus* from Pennsylvania ranged from 12.0 to 25.1 g with a mean of 16.7 g (Dunning 1992).

ECOLOGY AND BEHAVIOR

Distribution and abundance.—*Vireo gracilirostris* is confined to the main island of Fernando de Noronha and does not occur on any of the adjacent islets, the largest of which is Ilha Rata, where the elaenia exists but not the vireo. The birds are generally distributed throughout the island wherever there is forest, or at least scrub, but are absent from large areas in the center of the island that have been cleared for airport runways, fields, etc. The greatest numbers occurred in the forest around the famous phonolitic plug known as Morro do Pico, and in the forest that covered the western quarter of the island, where birds were truly abundant.

My only attempt to census vireos took place on the morning of 18 July 1973 from about 08:30 to 10:30 h while walking along the woodland trail at the western end of the island from the base of Morro Dois Abraços to the lighthouse at Alto da Bandeira, a distance of 2 km. During this time, I saw 31 vireos and counted 93 singing males. Although the birds are a favorite target of children who kill them to eat or purely for recreation (Nacinovic and Teixeira 1989), this is probably a minor source of mortality, and the species should not be in any danger as long as existing forested areas of the island are preserved.

Feeding and general behavior.—The Noronha Vireo is a curious and tame bird that allows close approach by humans and is generally quite tolerant of the presence of conspecifics. Birds that seemed to work too close to each other would sometimes snap their bills audibly at one another and move apart. I twice observed chases followed by weak singing by the "victor," but usually there was little aggressive behavior between birds, which often foraged in proximity to one another in considerable numbers. Birds in pairs, presumably mates, scold human intruders with great frequency while approaching closely.

TABLE 2

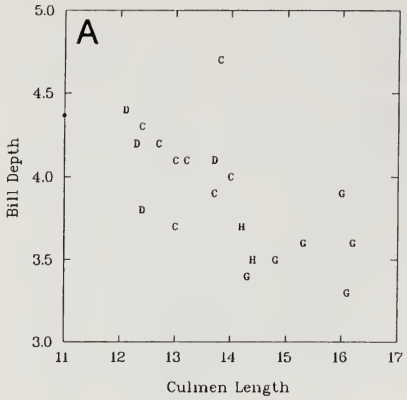
SKIN AND SKELETAL MEASUREMENTS (MM) OF *VIREO GRACILIROSTRIS* AND *V. OLIVACEUS*

Measurement	*V. gracilirostris*		*V. olivaceus*	
	Range	Mean	Range	Mean
1. Wing chord	60.2–66.5	62.9	62.4–73.5	68.1
2. Tail length	56.3–66.3	60.1	44.4–55.9	50.4
3. Culmen length	14.3–16.2	15.1	11.7–14.0	12.9
4. Bill depth	3.3–3.9	3.5	3.7–4.7	4.1
5. Cranium length	16.1–17.3	16.8	16.9–18.6	17.8
6. Cranium width	13.3–14.2	13.7	13.6–14.8	14.2
7. Bill length	16.2–17.7	16.7	14.0–16.6	15.6
8. Bill width	5.4–5.9	5.6	6.2–7.2	6.7
9. Pelvis width	8.0–9.0	8.6	9.1–10.5	10.1
10. Sternum length	11.3–12.3	12.0	14.9–18.0	16.9
11. Carina depth	3.4–4.6	4.0	5.3–6.4	5.9
12. Coracoid length	12.3–13.1	12.7	14.9–16.8	16.0
13. Humerus length	13.6–14.8	14.5	15.6–17.5	16.6
14. Ulna length	16.4–17.9	17.4	19.5–22.0	21.0
15. Carpometacarpus length	8.5–9.2	9.0	10.2–11.9	11.3
16. Femur length	13.2–14.5	14.2	14.1–15.9	15.1
17. Tibiotarsus length	26.3–28.5	27.6	23.8–27.5	25.8
18. Tarsometatarsus length	19.6–21.3	20.6	16.7–18.9	18.1

Notes: Measurements 1–4 are from skins, the specimens of *V. olivaceus* being of South American *chivi* group. For measurements 1 and 2, N = 22; for measurements 3 and 4, N = 9 for *V. gracilirostris* and N = 13 for *V. o. chiva*. Measurements 5–18 are from skeletons, N = 8 for each taxon. The skeletons of *V. olivaceus* include four *V. o. olivaceus* from North America and 4 from South America that are labelled as being of the *chivi* group, although one is probably a misidentified northern migrant. When not a standard measurement or self-evident, the manner of taking each measurement is specified as follows: 4. At anterior margin of external nostril. 5. From nasofrontal hinge to posteriormost extent of braincase. 6. Greatest width. 7. From nasofrontal hinge to tip. 8. At posterior margin of bony nostril. 9. Across antitrochanters. 10. From midline of manubrial fork to posterior margin. 11. From the ventral sternal plate to tip of carina. 12. From head to external distal angle. 17. Including cnemial crest.

Oren (1984) wrote that the vireo was flexible in procuring food, which is always small arthropods, and may forage from the tops of the trees to the ground and in leaves, on trunks, or in inflorescences. He also noted that it habitually hangs head down. Analysis of stomach contents reported by Nacinovic and Teixeira (1989) revealed a variety of insect remains (Coleoptera, Hymenoptera, Orthoptera, and Trichoptera) and a few small fruits of Ulmaceae.

In my experience, although the birds did show some variability in feeding behavior, most individuals spent more time foraging on the undersides of leaves than in any other feeding activity. In their most characteristic pose, the birds would grasp the edge of a leaf in their feet and bend over upside-down to feed from the undersurface. One bird stayed in this position for 15–16 sec, gleaning insects the entire time. Another


A
Bill Depth
Culmen Length
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12
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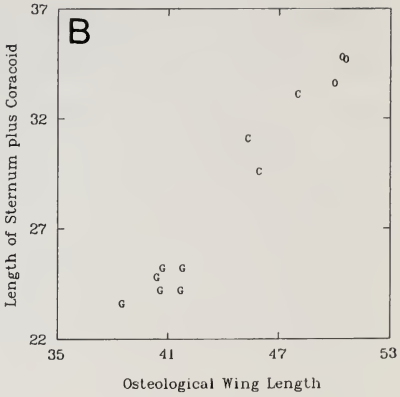
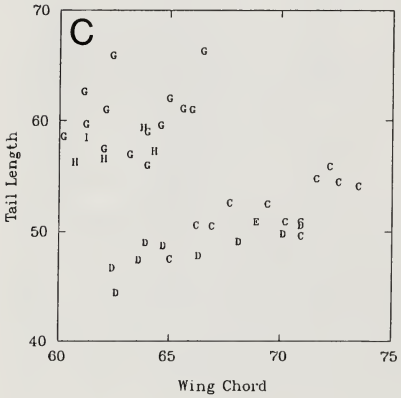

B
Length of Sternum plus Coracoid
Osteological Wing Length
37
32
27
22
35
41
47
53


C
Tail Length
Wing Chord
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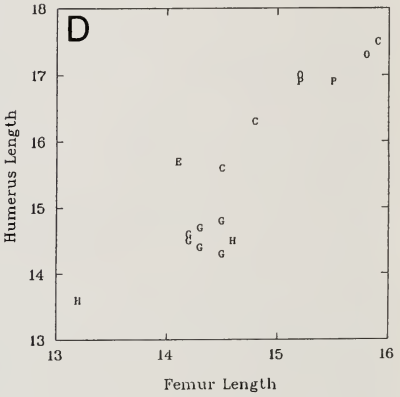
60
50
40
60
65
70
75


D
Humerus Length
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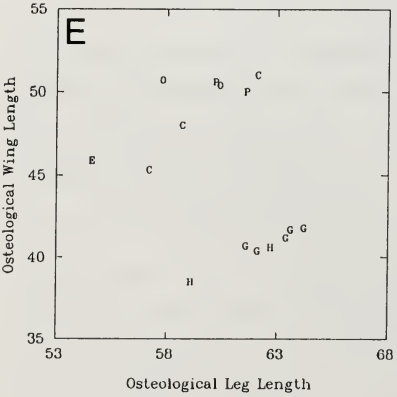
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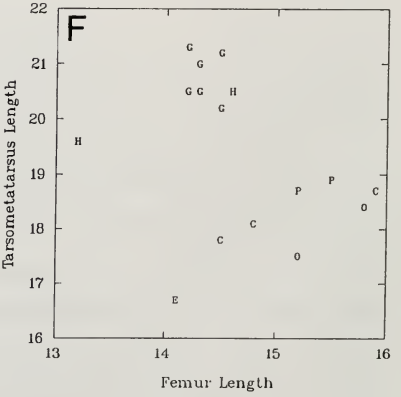
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bird was observed feeding upside-down from the flowers of an *Erythrina* tree. Three representative feeding bouts on the underside of leaves involved 32 gleaning movements in 2 min, 54 in 2 min, and 22 in 65 sec, for rates averaging between 16 and 27 capture movements per min. The main food appeared to be tiny "whiteflies" (probably Homoptera, Aleyroididae) that were often present in myriads. The long, slender bill, and especially the very long tail of *V. gracilirostris,* which would act as a counterbalance, appear to be specializations that facilitate feeding in this distinctive manner.

Foraging by hanging from leaves has been reported in several other species of *Vireo* and *Hylophilus* (Remsen and Robinson 1990:148). In a study of foraging behavior of forest birds in the eastern United States, Robinson and Holmes (1982:1924) found that Red-eyed Vireos (*V. olivaceus*) occasionally would forage by hanging from a leaf or twig (7.1% of observed prey capturing maneuvers vs 0.4–2.4% in all other species except Black-capped Chickadees, [*Parus atricapillus*], which used this technique in 28.7% of observed captures). Thus, the Noronha Vireo appears to have capitalized on a foraging technique that is present in its ancestral stock, but is used much less frequently.

Twice I saw birds make long hawking flights after insects, once a bird hovered over a leaf and gleaned from the upper surface, and only occasionally would a bird forage on trunks or limbs or capture larger insects. Birds were seen to hold prey, or once a piece of a leaf, under one foot while feeding on it. In one instance where several birds were seen feeding among roadside weeds, the majority seemed to be juveniles.

Noronha Vireos are probably very sedentary. One followed for 20 min did not move more than 15–18 m. A color-banded bird was seen several days after release only about 500 m from the original banding site.

Vocalizations.—The first description of the voice of the Noronha Vireo was by Nicoll, (1904:38) who noted that "it has a loud call-note, resembling the "*chizzick*" of a Wagtail," and also that "their loud, but by no

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FIG. 4. Bivariate plots of various skin and skeletal measurements (mm) of *Vireo gracilirostris* (G = males, H = females), *V. o. olivaceus* (O = males, P = females), *V. olivaceus chivi* (C = males, D = females, E = unsexed). In all cases, *V. gracilirostris* clusters separately from the other taxa, although there is overlap in some individual measurements. A. Skin measurements of bill depth versus culmen length. B. Combined lengths of sternum and coracoid versus combined length of humerus, ulna, and carpometacarpus. C. Skin measurements of tail length versus wing chord. D. Humerus length versus femur length. E. Combined length of humerus, ulna, and carpometacarpus versus combined length of femur, tibiotarsus, and tarsometatarsus. F. Length of tarsometatarsus versus length of femur.

means unpleasant, song somewhat resembled that of a pied wagtail [*Motacilla alba*]" (Nicoll, 1908:16).

Oren (1984:37) found the voice to be considerably variable, including simple notes reminiscent of a House Sparrow (*Passer domesticus*), a four-note song "typical of vireonids," and a high, thin whistle. Nacinovic and Teixeira (1989:723–724) noted only that the birds were loquacious, with a characteristic alarm "tschrrr, tschrrr."

The birds are generally quite vocal and possibly sing throughout the year, although by 8 August I noted that fewer individuals were inclined to sing than in July. At dawn on 16 July 1973, I was standing on the beach at the base of Morro do Pico when the entire forest around the peak burst into twittering like some giant seabird colony. This was caused by dozens of vireos singing—so many that individual songs could not be distinguished, and all melded into a chorus of vireos audible even over the roar of the surf.

On the basis of a poor-quality tape that I supplied, Barlow and Bortolotti (1989:1545, sonogram in fig. 5) were somewhat mislead as to the nature of the song in this species. "*Vireo gracilirostris* was represented by only 20 songs of either one syllable (18 times) or two syllables (1 time). Sixteen of 20 were downslurred, and three different syllables occurred in the sample of 20." From this they concluded that *V. gracilirostris* fits a pattern shown by other insular vireos that have a simpler song repertoire compared to mainland taxa. Reanalysis of the original tape with a more modern spectrograph (Barlow, in litt.), has revealed that the song of *V. gracilirostris* is more complex than had been interpreted previously. The results of this reanalysis will be published separately by Barlow.

To my ear, the full song of *V. gracilirostris* was reminiscent of that others of the Red-eyed Vireo group. I transcribed it as "*weet weet, chew-eyoo, whut whit,*" with the last note higher pitched. Songs could be quite variable, however, some being noticeably abbreviated. One bird that was watched for 2 min, during which it did not feed, gave a different call—"*seet, seet*" and "*seep-seep seedle seet.*"

The Noronha Vireo employs a variety of other vocalizations in different contexts. They frequently scold with a harsh "*skeeur*" or "*scree*" note (recordings indicate this has a buzzy quality and a 0.5 sec duration, Barlow in litt.). The response of a singing male to a playback of its song was a strident, harsher "*shree.*" One bird was seen to chase another, giving a short rattle, after which it moved through the trees singing feebly. Young peeped vociferously when fed. A nearly full-grown juvenile attended by two adults gave a "*tseep tseep*" call. One solitary, otherwise silent bird gave a little "*peep*" note just before defecating.

Reproduction and molt.—The breeding season of *Vireo gracilirostris* is

difficult to determine from the available data and is possibly correlated with local conditions rather than being on a strictly annual cycle. Apart from the gonad data with the specimens from the *Blossom* Expedition (which are often difficult to interpret), no information is available for the period from Janaury through May (Table 1).

Although Oren (1984) speculated that breeding was tied to the rainy season, Nacinovic and Teixeira (1989:724) surmised from field data and specimens in the Museu Nacional that the reproductive period coincides with the beginning of the dry season (September–October), a conclusion reached partly on the basis of their June specimens having small gonads. During my visit, however, I found a few adults still attending young at the end of July, and numerous individuals in the evanescent rusty juvenile plumage were present. There was no evidence of egg-laying at that time. Although some males had relatively enlarged testes, others did not, and no females had enlarged ovaries. The birds clearly were not breeding during my visit but must surely have been actively nesting in May and June of 1973.

Some males taken by the *Blossom* expedition in March and April were noted as "breeding" or had otherwise enlarged testes. Likewise, Murphy (1915) remarked that the pair he obtained in October was breeding. Oren (1984) noted the presence of many juveniles in December. Thus it seems that egg-laying either takes place twice a year or is irregular, although it is certainly not continuous.

The eggs of *V. gracilirostris* have never been observed or obtained by scientific collectors, although I was told by a resident of the island that the "*sibito*" may lay from two to five eggs. Higher numbers may be doubted, however, as virtually all tropical vireos have a clutch of only two (Barlow, in litt.).

An abandoned nest I found on 28 July was at the end of a limb about 5 m high in the lower story of a leafy tree on a steep hillside. It was suspended in a fork in typical vireo fashion and is composed of partially macerated leaves, fibers, rootlets, and spider webs. The outside diameter and depth are ca 64–72 mm by 52 mm, and the inside diameter and depth are ca 42 × 40 mm. This is similar to a nest described and illustrated by Nacinovic and Teixeira (1989), that was found 2.5 m up in a tree. Another old nest that I found was at the end of a small branch about 0.6 m long and 5 mm in diameter, about 6 m high in the middle of a tree.

Molt appears to take place mainly in July and August. The *Blossom* specimens taken in March and April are in worn or very worn plumage. Those that I obtained in July and August were usually in active molt, with fresh body plumage, and remiges and rectrices either new or in the process of being replaced. Numerous nearly tailless birds were seen during

this period. Murphy (1915) noted that his October pair was in fresh plumage with some body feathers still in sheath, yet by December Oren (1984) remarked that the plumage of adults was already very worn ("*muito gasta*").

DISCUSSION

The two largest genera of Vireonidae, *Vireo* and *Hylophilus,* have different centers of origin and diversity. *Hylophilus* would seem to be of purely South American derivation, with all 14 species occurring there, only four of which have entered Middle America and only two of which extend beyond Costa Rica. Conversely, the genus *Vireo* is most diverse in North and Middle America and the West Indies and hardly reaches South America at all. There are no endemic species of *Vireo* in continental South America, where the only breeding taxa are the Black-whiskered Vireo (*V. altiloquus*) along the northern coast, an extension of the *leucophrys* group of the Warbling Vireo (*V. gilvus*) into the Andes, and the *V. olivaceus chivi* complex. Because the last comprises the only resident populations of *Vireo* in the interior lowlands of South America, it is the only likely progenitor of *V. gracilirostris* on geographic grounds alone.

On the basis of genetic data from starch-gel electrophoresis, Johnson and Zink (1985) considered that the *Vireo olivaceus/chivi* group was specifically very distinct from the Yellow-green Vireo (*V. flavoviridis*) and that the *chivi* group diverged much more recently from *olivaceus,* possibly from northern migrants that failed to return to the north in the Pleistocene. They estimated the time of divergence between *olivaceus* and *chivi* at about 370,000 years ago, although this figure is based on a calibration that I regard as at best only a crude approximation and possibly erroneous. This does not affect the overall assessment that *olivaceus* and *chivi* are only weakly differentiated and that this differentiation took place in the geologically recent past, however.

Given the history of *V. o. chivi* hypothesized by Johnson and Zink, it naturally follows that *Vireo gracilirostris,* presumed to be derived from *V. o. chivi,* is likewise recent in origin. Despite this, not only is it a morphologically distinct species, but it is one of the more specialized members of the family, having diverged farther from its ancestral stock than any other member of the Red-eyed Vireo complex.

The long, slender bill and tarsus and the elongated tail appear to be warbler-like specializations for gleaning small insects from foliage. The long tail may function as a counterbalance during the upside-down posture commonly assumed when feeding on the undersides of leaves.

This relatively extreme specialization for a vireo has taken place in

isolation, without any serious competition from other species of birds. The only other arboreal land bird on Fernando de Noronha is the flycatcher *Elaenia spectabilis ridleyana,* which probably overlaps relatively little with the vireo in feeding habits. Although I saw elaenias feeding on "whiteflies" on the undersides of leaves by hovering, they were far less proficient than the vireos at using this food source and spent much less time so engaged. They also feed rather extensively on fruits, such as berries of *Lantana,* which the vireos apparently do not. The elaenia is only slightly, if at all, differentiated from its mainland relatives and appears to be a more recent arrival to the island.

Thus the Noronha Vireo evolved its specialized adaptations in the absence of interspecific competition. If competition actually affects morphological differentiation and subsequent speciation, in this case only *intra*specific competiton could have been involved. The founding population of vireos, upon colonizing an island in which all niches for arboreal insectivores were vacant, did not become more generalized so as to occupy a greater diversity of feeding opportunities, but instead appears to have evolved specializations for a more active, warbler-like lifestyle in order to feed on what is probably the most abundant or nutritious food source.

A similar evolutionary history was envisioned by Gill (1971) for the white-eyes (*Zosterops*) of the Mascarenes, where there are two sympatric species. Gill hypothesized that the first species to colonize became specialized for the richest food source (in this case nectar), from which the second colonizer, which is more of a generalist, was then excluded. The Noronha Vireo provides evidence that such an evolutionary history is possible and that a single species in isolation may become a specialist rather than a generalist.

ACKNOWLEDGMENTS

My visit to Fernando de Noronha was sponsored in part by the National Geographic Society (Grant 1105) and by the International Council for Bird Preservation. I am especially grateful to Bill Zimmerman for his beautiful execution of the frontispiece, and I must apologize for having delayed its appearance for so long. I thank Helen F. James for entering and plotting the data in Fig. 4. All data are from specimens in the National Museum of Natural History, Smithsonian Institution (USNM). For insightful comments on the manuscript, I am indebted to Jon Barlow and J. V. Remsen.

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COLOR PLATE

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Wilson Bull., 106(1), 1994, pp. 18–25

FEATHER IN AMBER IS EARLIEST NEW WORLD FOSSIL OF PICIDAE

Roxie C. Laybourne,[1] Douglas W. Deedrick,[2] and Francis M. Hueber[3]

Abstract.—Two pieces of amber containing portions of feathers were obtained from the Dominican Republic. Only one feather was preserved in such a way that it showed diagnostic characters. By comparing the plumulaceous barbules of the fossil with several species of non-passerines, the fossil was identified as a member of the family Picidae. Further comparisons indicate that the fossil was related closely to the Antillean Piculet (*Nesoctites micromegas*). This confirms a long presence of birds similar to *Nesoctites* on Hispaniola and documents the earliest New World fossil of Picidae. *Received 1 June 1993, accepted 14 Aug. 1993.*

The Palo Alto Mine in the Cordillera Septentrional of the Dominican Republic is well known for amber with inclusions of animal and plant remains. The amber occurs as angular-to-slightly-rounded fragments in consolidated carbonaceous fine silts and sands that accumulated in a marine environment. Analyses of assemblages of foraminifera found in association with the amber at Palo Alto indicate a minimum age of lower Early Miocene for the sediments (Baroni-Urbani and Saunders 1980).

Two pieces of amber from Palo Alto in the collections of the Dept. of Paleobiology, Smithsonian Institution, contain portions of feathers. These pieces of amber were referred to the senior author who has been identifying whole and fragmentary feathers from all parts of the world since the early 1960s. Characters denoting the family of birds have been discovered through her research on the micromorphology of the plumulaceous (downy) barbules (for feather topography see Fig. 1). It is the knowledge gained in the study of these barbules that has made it possible to identify hitherto unidentifiable feather material, including fossil feathers. One piece of amber (USNM 474728), described by Poinar et al. (1985), is 22.5 × 13.8 mm and contains a single pennaceous barb 11.9 mm long. There are no plumulaceous structures with which to make comparisons, and no diagnostic characters are visible. The more important of the two pieces of amber (USNM 469150) is 30.6 mm long × 7.5 mm wide and contains a partial feather 17.5 mm with the longest pennaceous barb 8.4 mm long. Identification of the feather was based on conformation of the plumulaceous barbs attached at the base of the feather, which were studied and

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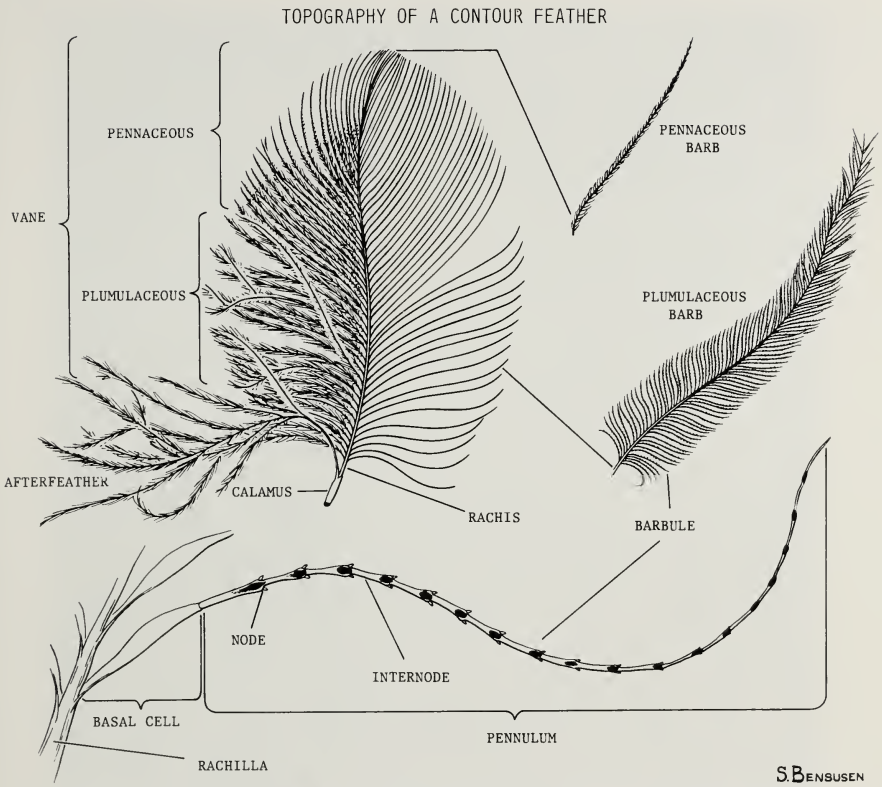

FIG. 1. Contour feather (flank) of Hispaniolan Woodpecker (*Melanerpes striatus*) depicting the parts of a feather (pen & ink by S. Bensusen).

photographed with the light microscope (Fig. 2). The length of the plumulaceous barbules varied from 1.09 to 1.54 mm, and the distance between the nodal structures proximal on the barbule varied from 0.021 to 0.023 mm. The villi on the basal cell are curved or scimitar shaped, a form unique to the Picidae (Brom 1991). The barbules are heavily pigmented and expanded at the nodes. These enlarged nodal structures bear slightly flared and transparent prongs at right angles to the node. One nodal structure clearly shows at least four prongs. The internodes are transparent.

When studying the microscopic structures of the downy barbules, a combination of characters is considered for each species studied. In this case, the microscopic study of these barbs and barbules indicated a nonpasserine bird from the following characters: the relative distance between the barbules (at the junction of the rachilla), the long basal cell, relative

FIG. 2. Photomicrograph (250×) of downy barbules of fossil feather.

width of the internode, nodal morphology, and the relative distance between the nodes. The fossil feather contained in USNM 469150 was compared with feathers of likely species of non-passerines that now occur in the area where the amber was found—Gray-headed Quail-Dove (*Geotrygon caniceps*), Narrow-billed Tody (*Todus angustirostris*), Broad-billed Tody (*Todus subulatus*), and Hispaniolan Trogon (*Priotelus roseigaster*). We also studied species not now occurring in the area, for example:

FIG. 3. Photomicrograph (250×) of downy barbules of Antillean Piculet.

FIG. 4. Photomicrograph (250×) of fossil feather showing pennaceous barbules at base feather.

Turquoise-browed Motmot (*Eumomota superciliosa*), Giant Hummingbird (*Patagona gigas*), Long-tailed Hermit (*Phaethornis superciliosus*), and White-mantled Barbet (*Capito hypoleucus*). The nodal structures on the plumulaceous barbules of only the trogon and the barbet were similar to those of the fossil feather. In the trogon, the distance between the nodes along the entire pennulum was greater; the pigmented nodal area and the

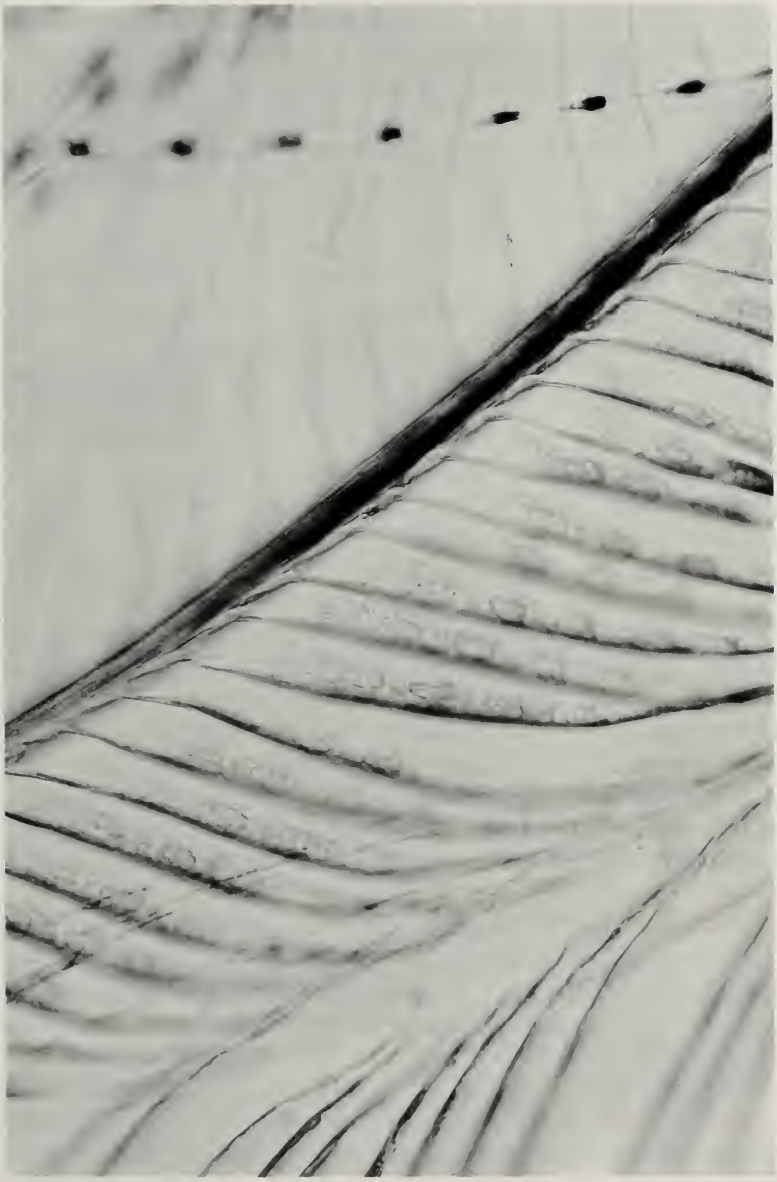

FIG. 5. Photomicrograph (250×) of Antillean Piculet showing pennaceous barbules at base of barbs from a wing covert.

transparent area around the node was smaller, and the width of the internode was not as wide as in the fossil sample. Although the barbet was more similar to the unknown than was the trogon, it differed from the fossil in having a shorter basal cell, more elongated pigmented area, more spinelike transparent areas outside the node, and shorter distance between nodes. Both the trogon and barbet lack villi. Because the barbet, a member of the Order Piciformes, was most similar to the fossil, we examined species related to that group that now occur in the area—the Hispaniolan Woodpecker (*Melanerpes striatus*) and the Antillean Piculet (*Nesoctites micromegas*). Both recent species were then studied and photographed with light (Fig. 3) and scanning electron microscopes. The Antillean Piculet had a long basal cell, wide internode, and villi characteristic of Picidae, and differed from the Hispaniolan Woodpecker in nodal morphology, shorter internode, and angle of the transparent area outside the pigmented node. In the Antillean Piculet this transparent area is almost at right angles to the node with rounded tips, whereas in the Hispaniolan Woodpecker the angle of the transparent area is more acute. The feather in amber closely matched a wing covert of the piculet in shape and size of the whole feather, and in the distribution of pigment in the basal pennaceous barbs (Figs. 4 and 5). Characters of the downy barbules of the piculet were indistinguishable from those of the fossil feather. To define the characters of the down of this group further, we studied four additional species—Rufous Piculet (*Sasia abnormis*) and Speckled Piculet (*Picumnus innominatus*) from the Old World and White-barred Piculet (*P. cirratus*) and Chestnut Piculet (*P. cinnamomeus*) from the New World. The fossil feather was most similar to the Antillean Piculet, and we conclude that it belongs to a bird closely related (at least congeneric) to that species.

Amber-bearing sediments of the Cordillera Septentrional are redeposited sediments of Upper Eocene age (Lewis 1980). However, analyses of assemblages of foraminifera at other sites across the basin of amber-bearing sediments indicate probable reworking and mixing of faunas of Eocene, Oligocene, and Miocene ages. This condition may apply to the flysch-like sediments of the whole area. The slightly abraded condition of the amber in the mines, particularly the stalactitic forms, suggests that the resins had been transformed into amber prior to being eroded from their original depositional sites as the toughness of amber relative to raw resins makes it less prone to heavy abrasion and fragmentation. Therefore, we conclude that the specimen of amber that contains the piculet feather is certainly older than lower Early Miocene, having been formed in and reworked from earlier terrestrial deposits into the marine. The nature of the mixed faunas of Miocene, Oligocene, and Eocene ages across the basin

extends the possible age of the amber to earliest Upper Eocene. The younger and older limits derive from the hypothesis that the amber was fully formed well before the beginning of the Miocene but no earlier than the beginning of the Upper Eocene. The consensus of geologists now working in the Dominican Republic favors the younger side of this time span, although more data are required. Regardless of the geologists' determination of the age of the amber in which this feather is preserved, this is the oldest known fossil of Picidae from the New World and the first pre-Pleistocene bird to be reported from the West Indies. Previous studies of fossil bones of Picidae have placed Picidae back to Middle Miocene (Olson 1985).

This report confirms a long presence of birds similar to *Nesoctites* on Hispaniola. This genus should be counted among the more ancient lineages of vertebrates in the West Indies, comparable to todies and the mammalian insectivores (Olson 1978). Long isolation of this piculet on Hispaniola has permitted differentiation to the extent that Short (1974) considered it to be a distinct tribe, Nesoctitini.

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CARCASSES OF ADELIE PENGUINS AS A FOOD SOURCE FOR SOUTH POLAR SKUAS: SOME PRELIMINARY OBSERVATIONS

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Abstract.—South Polar Skuas (*Catharacta maccormicki*) take eggs and young of Adélie Penguins (*Pygoscelis adeliae*) by scavenging and predation. We collected carcasses of penguins near Davis, East Antarctica, and examined them for damage and tissue removal by skuas. Progression of tissue destruction and removal was used to indicate successive areas of feeding. Organs and tissues from undamaged, fresh corpses were weighed to determine potential food quantities. Areas of initial attack were around the head. Subsequent damage was concentrated in the thoracic-abdominal regions, and around pelvic limb musculature. Such areas provided 19% (abdominal) and 12% (pelvic muscles) of the body mass. Because seabird eggs and chicks provide as much, if not more, energy as alternative foods (krill, fish) which require extended foraging, it is adaptive for skuas nesting near penguin colonies to forage there. *Received 4 Dec. 1992, accepted 13 May 1993.*

Foods eaten by South Polar Skuas (*Catharacta maccormicki*) vary among sites around Antarctica. In some areas, there may be a reliance on fish (e.g., Young 1963a, 1970; Pietz 1987) or, at coastal or inland sites, on bird species (e.g., Mehlum et al. 1988, Heatwole et al. 1991, Wang and Norman 1993). Elsewhere, as at some sites in East Antarctica, eggs and chicks of Adélie Penguins (*Pygoscelis adeliae*) are important in the skuas' diet. This may be particularly so for skuas with feeding territories near or within Adélie Penguin colonies, but skuas breeding some distance away from colonies may also take penguins (e.g., Green 1986, Norman and Ward 1990). Despite the varying extent to which South Polar Skuas depend on Adélie Penguins as a food source (e.g., Young 1963a, b; Maher 1966; Spellerberg 1975), their role as predators of penguins, particularly of eggs and chicks, has become well-established. However, little attention has been paid to the use that skuas make of penguin carcasses as a food resource, even though alternative foods or foraging strategies may be locally available.

This study describes patterns of feeding from corpses of Adélie Penguin chicks by South Polar Skuas. It includes description of the site of initial attacks, the sequence of tissue and/or organ use, and the subsequent carcass destruction.

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METHODS

During the 1990/1991 austral summer, carcasses of Adélie Penguins were collected at various sites in the Vestfold Hills area and were categorized by plumage as being chicks (guard or post-guard), subadults, or adults. On 4 January 1991, 101 penguin carcasses (damaged or otherwise) were collected in and around a colony on Hop Island (68°50′S, 77°42′E). This sample included 42 with subadult plumage (i.e., not hatched during the 1990/1991 season). A sample of 14 fresh, young chick carcasses was obtained at Hop Island on 8 January 1991. Collections were also made at Hawker Island (68°33′S, 77°51′E; 15 January 1991, 25 recently-dead chicks) and Magnetic Island (68°33′S, 77°54′E; 20 January, four young, four subadult and two adults). All carcasses were examined in detail for evidence of external damage (=skin break) associated with initial (procurement or killing) activities of skuas, and for subsequent disturbance or removal of underlying tissues, organs or body parts. Increased destruction was taken to indicate progressive use of carcasses as a food source (although not necessarily by the same skuas), as was removal of body parts (e.g., head, limbs, etc.). For complete carcasses, damage was assigned to 29 body regions but a further nine categories (including those for missing body parts) were used for incomplete corpses (see Fig. 3). However, in some summaries below, there has been an inevitable need to combine areas of attention.

To estimate potential food available to skuas from parts of penguin carcasses, apparently undamaged, fresh corpses (nine chicks, one adult) were collected at Magnetic Island on 19 January 1991. Each carcass was weighed (to 0.1 g). Pectoral and pelvic limb muscles (one side only, doubled in summaries below), submandibular and ventral cervical soft tissues (including tongue, trachea and esophagus to thoracic inlet), thoracic organs (heart, and lungs with associated major blood vessels), and abdominal organs (intestinal tract, complete stomach, liver and spleen, kidneys, adrenals and gonads) were removed and weighed separately (to 0.01 g).

For carcasses with damage, the locations of skin breaks and tissue and organ removal were examined by clustering analyses using PATN (e.g., Belbin 1990, 1991) to determine patterns of damage and hence sequences of carcass tissue utilization. Data from complete and all other carcasses were combined, and dendrograms developed, using the Bray-Curtis association measure and the UPGMA fusion strategy (with b set at -0.1, Belbin 1990).

RESULTS

Tissue, organ and body masses. —Organ and tissue masses are compared (Fig. 1) with body masses of intact Adélie Penguin chicks (of varying ages) and that of an adult. Simple correlations between organ masses, and between organ and body masses in each individual, were generally strong and highly significant ($r = 0.92$ to 0.99, $P < 0.01$–0.001, $N = 8$–10), but correlations involving stomach mass (although significant) were somewhat reduced (e.g., with submandibular and neck tissue, $r = 0.732$, $P = 0.016$), presumably reflecting differences in included contents. Although maximum stomach mass in a chick examined here was only 83.6 g, food deliveries to chicks may be about 20% of body mass (Croxall and Lishman 1987) and some 470 g of krill may be delivered to a 1 kg chick (Trivelpiece et al. 1987).

Abdominal organs formed 18.8% (± 3.7 SD, $N = 9$) of the mean body

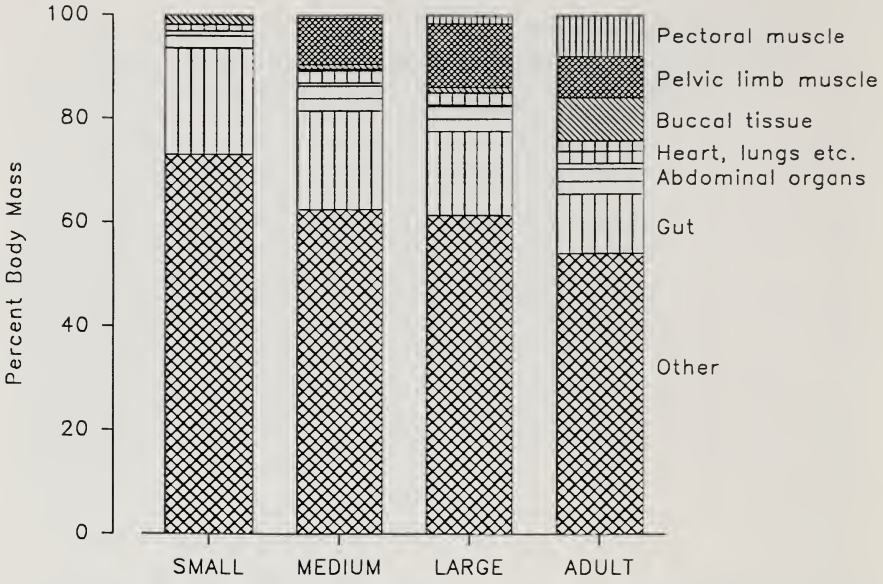

FIG. 1. Organ and tissue masses as percent of body mass in Adélie Penguins. One small chick (57.5 g), four medium-sized chicks (mean 261.9 g ± SD 114.4), four large chicks (780.5 g ± 273.3) and one adult (4370 g) were sampled.

mass. The stomach itself contributed 8.0% (±3.3, N = 10), the heart, lungs and associated vessels 4.4% (±1.1, N = 8), and the spleen, liver, kidney, adrenals and gonads 5.3% (±0.9, N = 9). Pelvic limb muscles (11.6%, ±1.7, N = 8) were important in determining the average carcass body mass, but pectoral muscles (2.1%, ±2.4, N = 8) and submandibular and ventral cervical soft tissues (1.8%, ±2.3, N = 10) were not.

Carcass utilization.—For the more extended series of 115 carcasses collected on Hop Island, 14 (12.2%, including 13 subadults from a previous season) had no obvious external damage and apparently had not been killed or fed on by skuas. External damage only was noted on 79 complete (i.e., not dismembered) corpses (chicks and subadults) from all sites, but of these most (71, 89.9%) had multiple injuries. Single areas of damage or attack were concentrated around the head or neck (seven instances). In corpses with more than surface damage, subsequent feeding was extensive and concentrated in the thoracic–abdominal regions. Thus, in the complete chick and subadult carcasses, of the 518 skin breaks and tissue or organ removal noted, 116 (22.4%) were in the head and neck region, while 283 (54.6%) involved the thoracic and abdominal skin, the underlying tissues and/or organs. In some instances, access to thoracic

material was achieved through abdominal skin breaks. Skuas paid little attention to the pectoral (8, 1.5%) and pelvic (35, 6.7%) regions, but did attack the pelvic limbs (84, 16.2%). At least 11 carcasses had broken spines, 12 broken necks, five had broken ribs, and three showed cranial breaks. There was no significant difference (t-test) apparent between mean numbers of damage areas in either the complete carcasses of chicks (7.57 $\pm$ 8.09) or those of subadults (7.37 $\pm$ 6.68), suggesting similar utilization patterns.

Increased feeding by skuas ensued around the abdomen and upper leg musculature, as indicated by the damaged penguin corpses (133 young and subadult, two adult) examined. Indeed, 489 (48.1%) instances of tissue damage or removal were in those areas. Removal of head (in 44 instances) and neck (24) apparently often followed initial feeding. Such destruction masked the possibly more extensive damage on the body parts removed. Examination of damage totals (discounting those involving removal of body parts) for major body areas (head, neck, thorax, pectoral, abdomen, pelvic and pelvic limb) showed significant differences (χ^2, $P < 0.0001$), with cell frequencies indicating that complete corpses had higher damage rates around the head and neck areas, and incomplete lower, than expected. Complete and incomplete carcasses had higher rates of damage in the pelvic limb area, but incomplete carcasses showed a higher incidence of damage, and complete carcasses lower, than expected in the pelvic area itself. Ultimately, all parts of the carcass were attacked, and remnant carcasses (cruciform) of leg and wing bones, and skull, were depleted of all soft tissues and/or dismembered.

This progression is also supported by pattern analyses. For all complete carcasses (Fig. 2), it is apparent that centers of damage exist around the head and neck, the thoracic region, and the abdomen (including the pelvis and pelvic limbs). Damage may be used to separate birds into four groups having tissue damage in the (1) head and neck region, (2) head and pelvic area, (3) neck, thorax, abdomen and pelvic area, and (4) those with damage around the pectoral region. Consideration of carcasses showing more extensive damage (Fig. 3) suggests that five groups exist, namely damage centered around the head (including its removal), a group with predominantly abdominal, pelvic and neck damage, a group showing thoracic and pectoral damage, one group having abdomen and pelvic areas removed, and a fifth group with major bone damage and removal.

DISCUSSION

Skuas are not well-adapted for flesh-eating. Unable to hold prey with their feet, they have to rip with the bill (Burton 1968). Nevertheless, throughout their range, South Polar Skuas are predators and/or scaven-

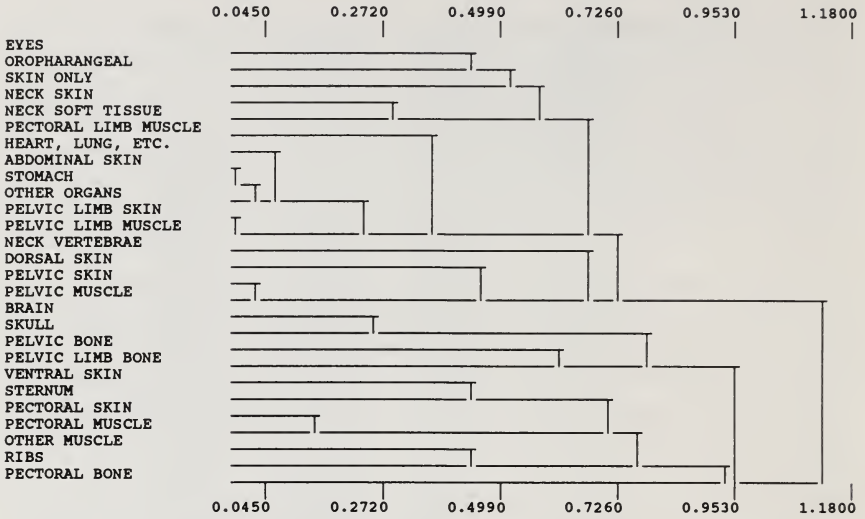

FIG. 2. Dendrogram showing clustering of areas of tissue damage in complete carcasses of Adélie Penguins (chicks and subadults) eaten by South Polar Skuas in the Vestfold Hills area, East Antarctica (Bray-Curtis association measure indicated, using Belbin 1990).

gers. Seabirds such as Adélie Penguins are included in their diet. In this study, Adélie Penguin carcasses with only external skin breaks, areas involved in procurement and killing or initial feeding, showed damage centered around the head, jaw, throat and eye. Bone damage may also have been associated with killing or later feeding. Various authors have suggested that skuas jump on terrestrial prey and drag young penguins away from creches. Initial attacks are then directed toward eyes, the skull or neck, with attention being paid to legs and the rectal area. Damage associated with removal of kidneys has also been noted (Wilson 1907, Sladen 1958, Burton 1968, Johnston 1973, Furness 1987, Robertson 1992). Very young Adélie Penguins are apparently eaten whole by skuas, or torn apart before ingestion, while carcasses of those three or more weeks of age are stripped to leave bones of the spine, pelvic girdle and limbs (Young 1963b, Müller-Schwarze and Müller-Schwarze 1973, 1977). Initial feeding in this study was concentrated, most particularly, in the thoracic and abdominal regions (Figs. 2 and 3), which may reflect both ease of access into soft tissue (thoracic material was also removed through abdominal skin breaks) and nutritional efficiency. Tissues in other body areas were then removed, although not necessarily in one feeding bout. Feeding on abdominal and thoracic organs may decrease carcass mass by some 40% and removal of pectoral and pelvic limb muscles by a further 14%. Carcass remnants from penguin chicks may represent only 8% of initial body mass

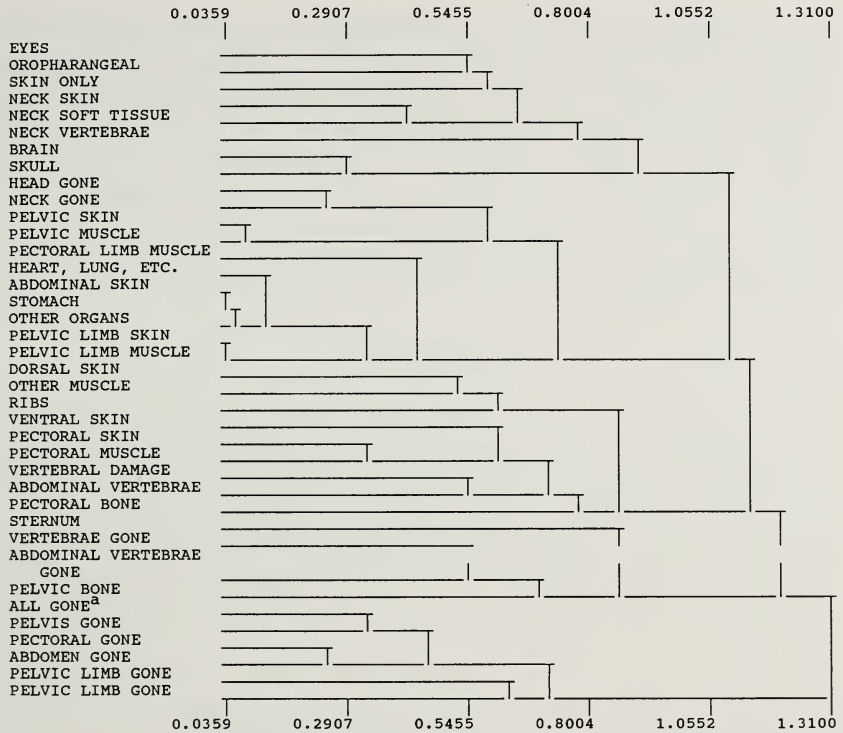

FIG. 3. Dendrogram showing clustering of areas of tissue damage and organ removal in Adélie Penguin carcasses eaten by South Polar Skuas in the Vestfold Hills area, East Antarctica (Bray-Curtis association measure indicated, using Belbin 1990). (a = whole pelvis removed.)

(Müller-Schwarze and Müller-Schwarze 1977), but Maher (1966) suggested that only 75% (i.e., some 645–790 g for birds sampled here) of a corpse was "edible."

Although the mean stomach mass in this series was some 47 g (and varied substantially with the age of the penguin), if stomach contents themselves represent a major food item (Müller-Schwarze and Müller-Schwarze 1977), then skuas may obtain up to 135 g of included food (mainly krill *Euphausia superba* and/or fish, predominantly *Pleuragramma antarcticum*) from a recently-fed chick in local colonies at about the time of these samples (Puddicombe and Johnstone 1988). Such foods may provide 3.8–5.4 (krill) to 4.8 (Dunn 1975) or 6.6–11.5 (fish) kJ/g wet weight (Clarke and Prince 1980). However, seabird eggs provide as much energy, and hatched chicks more as they develop. Short-tailed Shearwater (*Puffinus tenuirostris*) eggs provide 7.3 kJ/g wet weight, and chicks 5.2–

19.7 kJ/g (Fitzherbert 1985). Near fledging chicks of Double-crested Cormorants (*Phalacrocorax auritus*) may provide 9.2 (Dunn 1975) and Little Penguins (*Eudyptula minor*) 8.7 kJ/g (Gales and Green 1990). Fresh and recently-hatched chicks of Chinstrap Penguins (*Pygoscelis antarctica*) have calorific values of about 3.3 kJ/g and fledging chicks 9.2 kJ/g (Myrcha and Kaminski 1982). Increased fat reserves, rather than protein, would enhance the calorific value of chicks as prey, as would increased lipids in stomach fluids. Further, total calorific intake is improved by feeding from an individual chick rather than numbers of eggs. For this reason, it may be appropriate for skuas to move attention from eggs to chicks as they hatch and grow. On Magnetic Island, abandoned penguin eggs were not always eaten, although they were extensively scavenged before the hatching of chicks, which were not always eaten immediately after being killed.

Early in the skuas' breeding period, during incubation or when their chicks are small, penguin chicks may be killed but only lightly used by skuas (e.g., Brown Skua [*C. skua lonnbergi*], Hemmings 1990), with perhaps only the stomach being taken initially, before later carcass utilization (Melke 1975, Müller-Schwarze and Müller-Schwarze 1977, Furness 1987). This apparent surplus killing may allow the establishment of a larder that is managed as the breeding period continues (Pryor 1968, Müller-Schwarze and Müller-Schwarze 1973, Trillmich 1978). Such larders may provide for shortages of food after penguin chicks have fledged and departed, when developing skua chicks have increased food demands (and may scavenge by themselves within the feeding territory), or when adult, molted penguins leave breeding areas. Such corpses, and those of penguins dying during molt, may also provide food early in the following breeding season (indeed C. Pascoe, pers. comm. reported this at Hop Island in 1991/1992). The incidence of undamaged corpses of subadult penguins at Hop Island, from previous seasons, may support this. Such larders represent a management system particularly appropriate in Antarctic areas, where food deterioration rates are low.

Early in the season penguin chicks provide skuas an alternative to foraging for other foods (such as krill or fish, or other less-densely breeding avian prey), and later one providing more caloric value without extended foraging and associated energy expenditure. However, feeding on Adélie Penguin chicks depends on their availability, not only to skuas holding feeding territories which include breeding penguins but to others excluded from such areas. For skuas with ready access to chicks, management of carcasses (Müller-Schwarze and Müller-Schwarze 1973) may represent a useful strategy during the development of their own chicks, particularly since during the guard stages, penguin chicks may be less available (Maher 1966) and larger ones difficult to kill (Müller-Schwarze and Müller-Schwarze 1973). Although penguins chick carcasses contain more poten-

tial food mass and energy than individual alternative foods, they also represent a food reserve for times of shortages. Certainly such foraging is more energy efficient than kleptoparasitism (Maxson and Bernstein 1982). It may at times also be more efficient than extended flights in search of krill or fish. Young (1963b) reported periods away from the territory of up to 93 min, with some 140 g of fish being obtained in 52 min. In contrast, a skua took 6.5 min to kill a penguin chick of 1750–2000 g. For South Polar Skuas with penguins in their feeding territories, or for others without continued access to them, carcasses may be stripped with profit.

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STATUS AND HABITAT SELECTION OF THE HENSLOW'S SPARROW IN ILLINOIS

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ABSTRACT.—Henslow's Sparrows (*Ammodramus henslowii*), formerly abundant throughout Illinois, now are rare and local in occurrence there. Analyses of distribution and abundance patterns within a representative sample of grassland fragments showed that habitat area is the most important factor influencing Henslow's Sparrows in Illinois. Henslow's Sparrows rarely were encountered on grassland fragments less than 100 ha. However, in large fragments habitat structure also significantly influenced distribution and abundance patterns. Henslow's Sparrows preferred areas having tall, dense vegetation with a high proportion of residual standing dead plant material. Prescribed burning and mowing removed the tall, dense vegetation this species prefers and significantly reduced bird densities within parts of grasslands that had been recently managed. *Received 9 March 1993, accepted 20 July 1993.*

Henslow's Sparrows (*Ammodramus henslowii*) breed locally in southern Ontario and northeastern and east-central United States (Hands et al. 1989). Concern over the status of this grassland sparrow was first expressed when the National Audubon Society (NAS) included it in their 1974 Blue List on the basis of population declines in the northeastern United States and western Great Lakes region (Arbib 1973). It remained on the NAS Blue List from 1974–1981, and was changed to Special Concern from 1982–1986 (Tate 1986). In 1987, the Henslow's Sparrow was identified as a migratory nongame species of management concern by the United States Fish and Wildlife Service (USFWS), as a result of widespread population declines and its specific association with restricted/vulnerable habitats (USFWS 1987). More recently it has been designated an endangered or threatened species listing candidate (USFWS 1991). Recent analyses of data from the North American Breeding Bird Survey by the USFWS's Office of Migratory Bird Management suggests that the United States population of Henslow's Sparrows has decreased by over 68% between 1966 and 1991 (USFWS, unpubl. data).

Historically, Henslow's Sparrows in the midwestern states bred in native prairie habitat (Nelson 1876, Ridgway 1889, Cory 1909). However, they also inhabit a variety of other grassland habitats including hayfields, pastures, wet meadows, and old fields (Graber 1968, Skinner et al. 1984, Sample 1989). Litter density and depth (Wiens 1969, Robbins 1971, Kahl et al. 1985), standing dead residual vegetation (Zimmerman 1988, Sample

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1989), forb and woody stem densities (Wiens 1969, Kahl et al. 1985, Sample 1989), vegetation height and density (Skinner 1975, Skinner et al. 1984, Kahl et al. 1985, Sample 1989), and field size (Peterson 1983, Smith and Smith 1990) previously have been recognized as important components of Henslow's Sparrow habitat.

Loss of habitat has been implicated as the most likely factor causing declines in Henslow's Sparrow populations in the midwestern United States and elsewhere (USFWS 1987, Hands et al. 1989, Smith 1992). However, the relative importance of factors such as predation, competition, weather, and human disturbance remains poorly understood (Hands et al. 1989).

The objective of this paper is to identify habitat features that significantly influence distribution and abundance patterns for the Henslow's Sparrow in a highly fragmented midwestern landscape.

METHODS

I collected data from 86, 4.5-ha (300 m × 150 m), strip transects (Conner and Dickson 1980) within 24 grassland fragments in northeastern and north-central Illinois (1987–1990). Strip transects were dispersed so as to provide representative samples of the available habitat within fragments and were distant enough from one another to eliminate the possibility of counting the same bird on two different transects. I located transects in a manner designed to minimize within-transect habitat variability and to maximize distance from major habitat edges (to the extent possible as constrained by fragment size).

Study areas included native and restored prairies and non-native, cool-season grass and fallow fields ranging in size from 0.5 to 650 ha (see Herkert 1991a for a complete listing of study areas and fragment sizes). Dominant grass species from the native and restored prairie study areas included big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), panic grass (*Panicum* spp.), cord grass (*Spartina pectinata*), prairie dropseed (*Sporobolus heterolepis*), and upland sedges (*Carex* spp.). Dominant grass species from the non-native grassland areas included Kentucky bluegrass (*Poa pratensis*), meadow fescue (*Festuca pratensis*), smooth brome grass (*Bromus inermis*), timothy (*Phleum pratense*), orchard grass (*Dactylis glomerata*), and red-top (*Agrostis alba*). Plant species nomenclature follows that of Mohlenbrock (1986).

I censused each transect 3–4 times between 15 May and 30 June, between sunrise and 10:00 h CST, and recorded the locations of all territorial (singing) male Henslow's Sparrows. I conducted censuses at a rate of about 0.9 km/h (20 min/transect). I classified bird census transects as occupied or unoccupied. In order to eliminate the inclusion of transient individuals, only transects in which Henslow's Sparrows were encountered on two or more visits were classified as occupied.

Each year I chose 40 randomly located sites within each bird census transect for vegetation sampling. I sampled vegetation structure by passing a metal rod (0.6 cm diameter) through the vegetation and counted the number of contacts by live grasses, live forbs, and dead plant material in successive 25-cm intervals of height (cf Rotenberry and Wiens 1980). I measured nine vegetation variables from each bird census transect, including mean litter depth, mean grass height, mean vegetation height, mean number of total (live grass, live forb, dead plant material) vegetation contacts, mean number of total vegetation contacts between 0–25 cm,

percentage of live grass contacts, percentage of live forb contacts, percentage of standing dead residual plant contacts, and woody stem density. Measurements of vegetation structure were made between 10–25 May each year, with sampling beginning in the southernmost study areas and progressing northward.

I compared vegetative features of occupied and unoccupied transects using the Kruskal-Wallis test (nonparameteric equivalent of single classification ANOVA), and analyzed the effect of burning on Henslow's Sparrow abundance by comparing densities from three management categories for census transects at the largest prairie site (Goose Lake Prairie). The management categories included first growing season (1–3 months) immediately following burning (burn-I); second growing season (13–15 months) since last burned (burn-II); and three or more growing seasons (>25 months) since last burned (burn-III). Burns were conducted on April 13 of each year (1988–1990). Henslow's Sparrow densities were compared between mowed and unmowed transects within a 238-ha non-prairie study site. Management categories consisted of mowed and unmowed areas. Mowed sites were cut either in the late fall or early spring prior to the start of the breeding season (May 1), and unmowed sites were not cut for at least 12 months prior to the start of the breeding season. The effect of burning on the large prairie area was analyzed using repeated measures analysis of variance (Neter et al. 1985), because all six census transects on the large prairie site received all three burn management treatments in one of the three years of study (1988–1990) included in the burning analysis. On the non-prairie study site, however, all transects did not receive both mowed and unmowed treatments; therefore the effect of mowing at this site was analyzed using traditional analysis of variance (Sokal and Rohlf 1981). All analyses were performed using SAS version 5 (SAS 1985).

RESULTS

Henslow's Sparrows were recorded from 13 (15%) of the 86 census transects. There was no apparent preference for native or restored prairie or non-native grasslands ($\chi^2 = 0.16$, df = 1, $P > 0.69$) with Henslow's Sparrows being recorded from a nearly equal number of native or restored prairies and non-native grasslands (6 out of 44 prairie transects and 7 out of 42 non-native transects). Occupied prairie transects were dominated by sedges, prairie dropseed, and cord grass and occupied non-native transects were dominated by meadow fescue and bluegrass. The initial comparison of vegetation features of occupied and unoccupied transects for all grassland areas revealed few significant differences (Table 1). Occupied transects tended ($0.05 < P < 0.10$) to have a greater vegetation density at heights between 0 and 25 cm and a higher percentage of standing dead residual vegetation than unoccupied transects (Table 1). The greatest difference between occupied and unoccupied transects, however, was the size of the grassland in which the transect was located. Henslow's Sparrows were far more likely ($P < 0.0001$) to occupy transects that were located in large grasslands, suggesting that grassland size may be the most important feature influencing Henslow's Sparrow habitat occupancy over the range of grassland sizes included in the study.

In order to eliminate the influence of grassland area on Henslow's

TABLE 1

MEAN VALUES AND STANDARD ERRORS (SE) FOR HABITAT ATTRIBUTES IN OCCUPIED AND UNOCCUPIED HENSLOW'S SPARROW CENSUS TRANSECTS LOCATED IN 24 GRASSLAND FRAGMENTS IN ILLINOIS

	Unoccupied		Occupied	
	Mean	SE	Mean	SE
All grassland areas (0.5–650 ha)				
Litter depth (cm)	2.75	0.23	3.08	0.36
Grass height (cm)	29.92	1.40	29.45	2.92
Vegetation height (cm)	57.41	3.30	49.27	4.92
No. contacts—total	4.95	0.28	5.92	0.58
No. contacts <25 cm	3.59*	0.19	4.81*	0.57
Woody stem density (stems/m^2)	1.23	0.31	1.72	0.83
Contacts—live grass (%)	21.02	3.19	20.31	7.38
Contacts—live forbs (%)	6.33	1.48	2.58	1.14
Contacts—standing residual dead (%)	27.76*	3.12	45.69*	8.75
Grassland area (ha)	87.20***	17.94	420.56***	62.71
Large grassland areas (150–650 ha)				
Litter depth (cm)	1.97	0.34	2.96	0.36
Grass height (cm)	19.77**	1.99	27.47**	2.33
Vegetation height (cm)	30.09**	7.23	47.23**	4.88
No. contacts—total	2.63***	0.57	5.75***	0.60
No. contacts <25 cm	2.15***	0.47	4.95***	0.60
Woody stem density (stems/m^2)	3.30	1.69	1.68	0.90
Contacts—live grass (%)	30.77	14.35	21.96	7.82
Contacts—live forbs (%)	7.68	4.00	2.80	1.21
Contacts—standing residual dead (%)	13.61**	4.79	45.00**	6.48
Grassland area (ha)	534.40	76.53	445.50	62.56

* $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$, Kruskal-Wallis test.

Sparrow habitat selection, habitat features of occupied and unoccupied transects were compared only for grasslands greater than 150 ha in size. This comparison revealed several significant vegetative differences between occupied and unoccupied transects. On large grasslands, Henslow's Sparrows occupied transects that had vegetation that was significantly taller (both mean grass and total vegetation heights), more dense (especially within 25 cm of the ground), and with a higher proportion of residual standing dead plant material than unoccupied transects (Table 1).

Burning had a significant effect on Henslow's Sparrow distribution and abundance on the large prairie study area ($F = 12.90$, $P < 0.002$). Henslow's Sparrows were never encountered on transects located in recently burned areas (Fig. 1). Moreover, average Henslow's Sparrow densities on

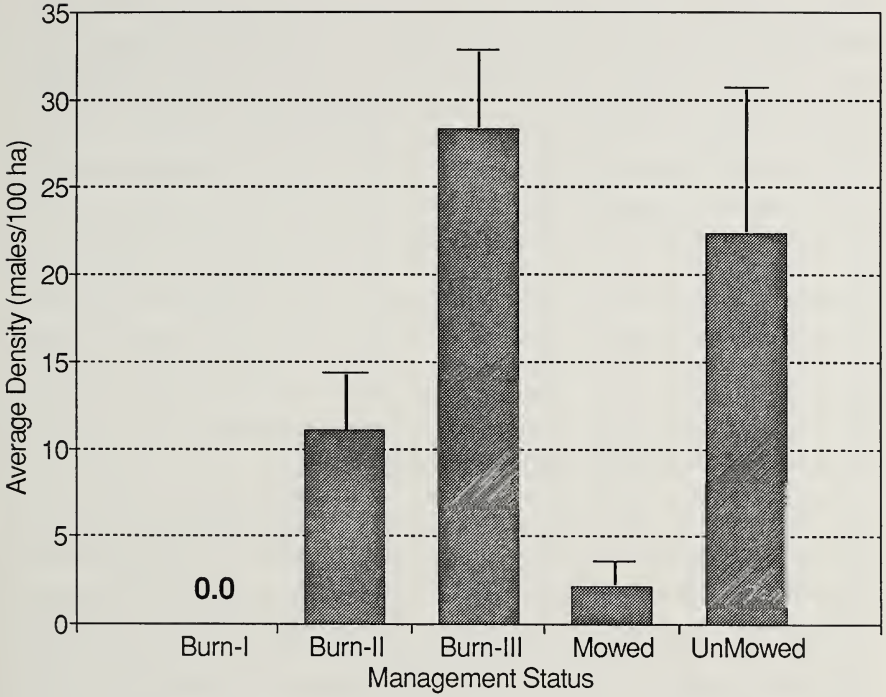

FIG. 1. Average densities of Henslow's Sparrows in census transects located in large managed grassland areas in Illinois. Bars indicate one standard error.

areas in their second growing season post-fire (burn-II) were less than half their densities on transects in their third or greater growing season post-fire (burn-III) (Fig. 1). Mowing also had a significant influence on Henslow's Sparrow abundance within the non-prairie grassland area ($F = 7.26$, $P < 0.025$). Although Henslow's Sparrows did not completely avoid mowed areas, average densities on mowed areas were nearly 90% less than they were on unmowed areas (Fig. 1).

DISCUSSION

Prior to 1900, the Henslow's Sparrow was considered to be abundant in Illinois (Herkert 1991b) and was among the most numerous prairie bird species in some parts of the state (Ridgway 1873). Ridgway described the Henslow's Sparrow as "much more common" than the Grasshopper Sparrow (*Ammodramus savannarum*) with only the Eastern Meadowlark (*Sturnella magna*) and Dickcissel (*Spiza americana*) being more abundant than it in 1871 at Fox Prairie, Richland County, Illinois. Nelson (1876) also considered the Henslow's Sparrow to be a common summer resident

in the prairies of northeastern Illinois, and more recently, Ford (1956) considered it a common summer resident in the northeastern part of the state. Between the late 1950s and the late 1970s, however, populations of the Henslow's Sparrow and several other grassland birds are believed to have declined substantially in Illinois (Illinois Natural History Survey 1983). Periodic surveys conducted by R. R. and J. W. Graber between 1957 and 1979 suggested that the Henslow's Sparrow population in Illinois may have declined as much as 94% during this period. The Graber's attributed the decline to a 65–75% decrease in grassland habitat and a concurrent 75% decline in average density within remaining grassland areas in Illinois (Graber and Graber, unpubl. data). The Henslow's Sparrow is presently a very local summer resident in Illinois (Bohlen 1989) and is listed as a state-threatened species (Herkert 1992). Henslow's Sparrows have recently (since 1980) been reported as summer residents in 14 of Illinois' 102 counties (Herkert 1992).

In many parts of their range, Henslow's Sparrow populations have often been described as somewhat unstable with numbers fluctuating from year to year (e.g., Hyde 1939, Wiens 1969, Robbins 1971). In Illinois, their appearance is also somewhat sporadic, especially in the southern part of the state (T. Fink, pers. commun.). In a few protected grassland areas in northern Illinois, Henslow's Sparrows are fairly common and are regular breeders. In the southern part of the state, however, Henslow's Sparrows occur sporadically in fescue and orchard grass fields in some years and are completely absent from this part of the state in other years despite the continued presence of similar habitat (T. Fink, pers. commun.). The largest known population in the state occurs on Illinois' largest native prairie remnant (Goose Lake Prairie, 650+ ha) where 15 to 55 pairs have bred consistently since at least the early 1970s (Birkenholz 1972, 1975, 1983, Birkenholz pers. commun., Herkert unpub. data). No other sites in Illinois are known to have more than 15 pairs of Henslow's Sparrows (Illinois Dept. of Conservation, unpubl. data).

In Illinois, Henslow's Sparrows choose habitats of specific vegetation structure and grassland size. Henslow's Sparrows were almost completely restricted to large grassland areas, occurring on only one grassland less than 100 ha. The general lack of significant structural differences between occupied and unoccupied transects when the full size range of grassland areas was compared (Table 1) further suggests that grassland size is the major factor influencing Henslow's Sparrow habitat selection in Illinois and possibly other highly fragmented Midwestern states. In other parts of their range, Henslow's Sparrows have also been shown to require relatively large grassland areas. In New York, Smith and Smith (1990) showed that this species requires pastures at least 30 ha in size. In Missouri,

Samson (1980) estimated that between 10 and 100 ha of prairie habitat were required to maintain viable populations of Henslow's Sparrows, although the methods used to derive this estimate are not clear.

The comparison of habitat attributes from occupied and unoccupied transects for large grassland areas (Table 1), however, shows that vegetation structure is also important in determining Henslow's Sparrow distribution and abundance patterns within tracts. Henslow's Sparrows inhabit large grassland areas that have tall, dense vegetation and a high percentage of standing dead residual plant cover.

Henslow's Sparrows have often been described to breed in "loose colonies" (Hyde 1939, Graber 1968, Wiens 1969, Johnsgard 1979); therefore, this species may avoid small grassland areas large enough for a single pair but not large enough for a "colony." In Illinois, this species is sometimes found in loose colonies but also occurs as single pairs. Sample (1989) described a similar pattern in Wisconsin, where Henslow's Sparrows also occur both in loose colonies and individually. Moreover, Smith (1992) has suggested that Henslow's Sparrows are not more colonial than other sparrows but only appear colonial as a result of clumping of suitable habitat. In any case, coloniality is unlikely to be a major reason for Henslow's Sparrow avoidance of small grassland areas, because many of the small grasslands that were unoccupied by this species appear to be large enough for several pairs. Henslow's Sparrow territory sizes have generally been estimated to be less than 1 ha (e.g., 0.6 ha, Wiens 1969; 0.3 ha, Robbins 1971). With a territory requirement of this size, grassland areas (with suitable habitat) as small as 10 ha should be large enough for several pairs, and yet Henslow's Sparrows are regularly absent from grassland areas much larger than this in Illinois.

Grassland management also significantly influences Henslow's Sparrow distribution and abundance patterns within grassland areas. Henslow's Sparrows are strongly influenced by prescribed burning of managed grasslands. In large native grasslands, burning prevents the establishment of Henslow's Sparrows in the summer immediately following spring (and probably fall) burning and significantly lowers densities in the ensuing year as well (Fig. 1). In Illinois, densities of Henslow's Sparrows in grasslands in their second growing season (13–16 months) following spring burning were roughly half of comparable densities in grasslands areas that have at least three growing seasons following burning (Fig. 1). This avoidance of recently burned areas is consistent with other research that has shown this species prefers relatively undisturbed, tall, dense vegetation (Skinner et al. 1984; Kahl et al. 1985; Zimmerman 1988, 1992; Sample 1989).

Regular mowing of the large non-prairie study area also significantly

reduced Henslow's Sparrow densities (Fig. 1), despite the fact that this mowing occurred outside of the breeding season. Studies in other regions and habitats, however, suggest that Henslow's Sparrows may use annually mowed or hayed areas (e.g., Hyde 1939, Smith and Smith 1990, DeNeal 1991). In New York pastures, Smith and Smith (1990) found no relationship between mowing and the occurrence of Henslow's Sparrows as long as mowing was undertaken after the nesting season. Additionally, reports of Henslow's Sparrows from midwestern hayfields (e.g., Hyde 1939, Graber and Graber 1963, DeNeal 1991) imply that this species can use annually mowed areas as long as the vegetation has had a chance to grow to an acceptable height and density prior to the breeding season. However, despite the presence of Henslow's Sparrows in some midwestern hayfields, the frequency of disturbance in these areas very likely severely reduces, if not precludes, successful nesting in these habitats (e.g., Warner and Etter 1989, Bollinger et al. 1990, Frawley and Best 1991).

Because of the large area requirement and avoidance of recently burned or mowed areas, grassland management for Henslow's Sparrows must be directed toward providing large unburned and/or unmowed areas. However, since grassland maintenance (Anderson 1970, Bragg 1982) and several other grassland bird species (Skinner 1975, Skinner et al. 1984, Herkert 1991a) are dependent on periodic fire or mowing for habitat maintenance, the optimal grassland management system would be a rotational system of burning or mowing in which subsections of large grasslands are managed on a regular rotating schedule as has been suggested for Henslow's Sparrows in Kansas (Zimmerman 1988). A rotational management system would ensure the availability of suitable habitat for Henslow's Sparrows as well as provide habitat for bird species that prefer short grass areas (Herkert 1991a). Just how large these units should be, however, is not clear. Based on incidental observations in Kansas, Zimmerman (1988) suggested that management units be at least 30 ha. My own incidental observations in Illinois show that Henslow's Sparrows may occasionally be found in small patches ($\sim$1 ha) of unburned prairie that occur within a much larger ($\sim$120 ha) matrix of burned prairie. However, whether these birds were mated or successfully reproduced in these small patches is not known. Nevertheless, given the sensitivity of this species to reduced habitat area and specific habitat requirements, management units should be at least 20–30 ha to be most effective. On large grassland areas (>100 ha) 20–30% of the area should be burned (or mowed) each year in a rotating series.

Finally, although the mechanisms causing Henslow's Sparrow declines remain poorly understood, conservation and management efforts directed toward protecting and/or establishing large grassland areas, with the spe-

cific habitat requirements this species prefers, offers the most promising approach to conserving and managing populations of this species.

ACKNOWLEDGMENTS

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TO: Members of the Wilson Ornithological Society

This past year the Council of the Wilson Ornithological Society has considered revision of the Wilson Ornithological Society's Bylaws and Constitution. By unanimous vote the Council has approved the consideration of two changes in our Bylaws and one Amendment to the Constitution. Final decision on these changes will be accomplished by a vote of our Membership during the annual meeting of the Wilson Ornithological Society in Missoula, Montana, 22–26 June 1994. The proposed changes will, (1) make changes in the Bylaws that permit the Council to set the fiscal year to a time period more in accord with receipts and expenditures that occur during the year, and (2) make changes in the Bylaws and Constitution relative to how new members may join the Society to reflect more closely what is actually practiced by the Society for the past two decades.

Suggested changes in the Wilson Ornithological Society Bylaws and Constitution:

1. **Repeal** of Bylaw 7 which reads: "The fiscal year of the Society shall be the calendar year." This will permit the Council to set the fiscal year.

2. **Repeal** item 5 of Bylaw 8, which establishes agenda items for the annual meeting. Item 5 reads: "Election of members."

3. **Amend** Article II, Section 2, by replacing the italicized wording with the boldfaced sentence. Replace "Any person who is in sympathy with the objectives of the Society *may be nominated for membership. Nominations and applications for membership shall be made through the Treasurer. Applications for membership shall be endorsed by at least one member.*" with "Any person who is in sympathy with the objectives of the Society **may become a member by submitting an application and appropriate dues to the Treasurer.**"

Items 2 and 3 reflect past practices that are no longer followed, and should be removed from the Constitution and Bylaws, or followed. Item 1 will allow the Council to set the fiscal year to 1 July–30 June which better fits the Society's annual financial cycle.

Please be prepared to vote on these three changes at our annual meeting in Montana.

Sincerely,
Richard N. Conner
President, The Wilson Ornithological Society

Wilson Bull., 106(1), 1994, pp. 46–54

REPRODUCTIVE SUCCESS OF NEOTROPICAL MIGRANTS IN A FRAGMENTED ILLINOIS FOREST

ERIC K. BOLLINGER[1] AND ERIC T. LINDER[1,2]

ABSTRACT.—In June–July 1991–1992, we replicated the mist-netting methods of Robinson (1988, 1992), who captured birds in forest fragments adjacent to Lake Shelbyville in east-central Illinois in 1985–1986. Of all forest-interior Neotropical migrants that were captured, a much high proportion were hatching year (HY) birds in 1991–1992 (29%) than in 1985–1986 (8%), indicating higher reproductive success. The numbers of Brown-headed Cowbirds (*Molothrus ater*) and the frequency of their parasitism were significantly lower in 1991–1992 than in 1985–1986. However, despite these improvements, reproductive success for Neotropical migrants was still low, presumably because of high levels of nest predation. A significantly lower percentage of adult birds captured in 1991–1992 were forest-interior Neotropical migrants than in 1985–1986 (35% vs 48%). *Received 22 March 1993, accepted 16 July 1993.*

In the past 20 years, there has been a marked increase in concern over the apparent population declines of many species of birds that breed in temperate North America and winter in the tropics (Neotropical migrants) (e.g., Briggs and Criswell 1978, Keast and Morton 1980, Robbins et al. 1989b, Askins et al. 1990, Hagan and Johnston 1992). These declines have tended to be most severe for species nesting in the interior of larger tracts of forest (i.e., forest-interior species; Terborgh 1989, Askins et al. 1990).

Forest fragmentation on the breeding grounds and deforestation in the tropics have frequently been mentioned as likely causes of the population declines of these birds (Askins et al. 1990, Terborgh 1992). On the breeding grounds, forest fragmentation reduces not only the quantity of habitat but also the suitability of that which remains for forest-interior Neotropical migrants (Whitcomb et al. 1981, Robbins et al. 1989a). Birds nesting in small forest fragments often suffer from high levels of brood parasitism by Brown-headed Cowbirds (scientific names given in Appendix I; Chasko and Gates 1982, Brittingham and Temple 1983, Robinson 1992), nest predation (Gates and Gysel 1978, Wilcove 1985, Wilcove et al. 1986, Temple and Cary 1988, Yahner and Scott 1988, Robinson 1992), and, perhaps, competition from non-forest or forest-edge species that invade the interior of small forest fragments (Ambuel and Temple 1983, Wilcove and Robinson 1990).

Perhaps nowhere have these detrimental effects been documented more dramatically than in the small forest fragments adjacent to Lake Shel-

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byville in east-central Illinois. Here, Robinson (1988, 1992) and Wilcove and Robinson (1990) documented extremely high levels of nest parasitism and nest predation in 1985–1986. For example, 76% of all nests of Neotropical migrants were parasitized by Brown-headed Cowbirds, with an average of 3.3 cowbird eggs per parasitized nest. Approximately 80% of all open-cup nests were destroyed by predators. As a result, this study has frequently been cited as a "worst case scenario" (Robinson 1990) of the detrimental effects of forest fragmentation on the breeding grounds for Neotropical migrants (e.g., Terborgh 1989, 1992; Roth and Johnson 1993).

In 1991–1992, we investigated reproductive success of Neotropical migrants to determine whether population sizes of Neotropical migrants had declined in these woodlots as a result of poor reproductive success and to determine if reproductive success was still as low as Robinson had found in 1985–1986. To answer these questions, we used Robinson's (1992) methodology for his midsummer mist-net samples.

STUDY AREA AND METHODS

Our study sites were three small woodlots (14-, 25-, and 65-ha) bordering Lake Shelbyville in Shelby and Moultrie counties, east-central Illinois (39°N, 88°W) and were the same sites studied by Robinson (1992). Efforts were concentrated in the largest woodlot, a 65-ha fragment (known as "the Boot") bordered by the lake to the north and by corn and soybean fields to the south. This woodlot is dissected by numerous intermittent streams with large white oaks (*Quercus alba*) scattered among dense young oaks and hickories (*Carya* spp.) on the ridge tops (see Linder 1992, Robinson 1988 for more details).

We mistnetted birds using the methodology of Robinson (1992 and pers. commun.) as closely as possible. We relocated Robinson's netlines and opened our nets at approximately the same places and times as he did in 1985–1986. We also netted the same areas for two consecutive years (1991 and 1992) as did Robinson. Between 15 and 25 mist-nets (black, 12 m, 36 mm mesh, 4 tier) were strung end-to-end along the netline and opened for three consecutive days from 06:00–12:00 h EDT. After the third day, the nets were moved to the next adjacent area. A total of five areas was sampled. Netting began on 20–21 June after the primary breeding season for most forest-nesting passerines and ended on 20–24 July before fall migration. Each area was sampled twice, once between 20 June–5 July and once (two weeks later) between 6–24 July.

All birds that were captured were banded with U.S. Fish and Wildlife Service aluminum bands, aged by plumage characteristics and skull pneumatization (Pyle et al. 1987, USFWS 1991), measured, and released. Birds were aged as either adult, "after-hatching-year" (AHY), or recently fledged, "hatching-year" (HY) birds. Compared to Robinson's studies, we spent relatively little time searching for nests or recently-fledged family groups.

We compared our mist-netting data with those of Robinson primarily through chi-square (χ^2) tests of the numbers of birds caught. Tests have one degree of freedom unless noted otherwise. We pooled data from 1991 and 1992 as Robinson did for 1985 and 1986. We used data published in Robinson (1988 and 1992) where possible and Robinson's unpublished data otherwise. We have followed the categorizations of Whitcomb et al. (1981) and Freemark and Collins (1992) to distinguish Neotropical migrant species from permanent

TABLE 1

HATCHING YEAR (HY): ADULT (AHY) RATIOS FOR FOREST-INTERIOR NEOTROPICAL MIGRANTS IN MIST-NET SAMPLES FROM LATE JUNE THROUGH MID-JULY, IN BOTH 1985–1986 (ROBINSON 1992) AND IN 1991–1992 IN FOREST FRAGMENTS ADJACENT TO LAKE SHELBYVILLE, ILLINOIS

Species	HY : AHY ratio	
	1985–1986	1991–1992
Great Crested Flycatcher	0.1 (19)[a]	0.6 (13)
Eastern Wood-Pewee	0.2 (12)	0.9 (13)
Acadian Flycatcher	0.0 (5)	0.2 (15)
Wood Thrush	0.1 (46)	0.6 (21)
Red-eyed Vireo	0.0 (2)	0.6 (19)
Kentucky Warbler	0.3 (14)	0.0 (8)
Worm-eating Warbler	0.0 (4)	1.0 (2)
Ovenbird	0.0 (11)	0.3 (13)
Louisiana Waterthrush	0.5 (3)	1.0 (2)
Scarlet Tanager	0.0 (7)	0.2 (13)
Total HY : Total AHY	0.1 (123)	0.4 (119)

[a] Numbers in parentheses are total numbers caught (HY + AHY) for each species.

residents and short distance migrants. These references were also used to categorize species as either "forest interior" or "edge" species (see Appendix I). Permanent residents and short-distance migrants are referred to collectively as "local" species.

We used HY percentages (or HY : AHY ratios) as our index of reproductive success. We assume that high reproductive success will result in a high proportion of HY birds in our mist net samples. We believe that HY percentages (or HY : AHY ratios) provide a reasonable index of reproductive success and population sizes for comparative purposes between Robinson's data and our own. Others (e.g., Karr 1981, Robinson 1992) have discussed the benefits and limitations of using mist-netting data to infer breeding success and population dynamics. Therefore, we will attempt to "generalize cautiously" (Robinson 1992:416) from our data.

RESULTS

For all forest interior species combined, we captured a significantly higher proportion of HY Neotropical migrants (29% of 119 Neotropical migrants) in 1991–1992 than did Robinson in 1985–1986 (8% of 123) ($\chi^2 = 18.1$, $P < 0.001$). Furthermore, our HY : AHY ratios were higher for nine of the 10 species of Neotropical migrants reported by Robinson (1992, Wilcoxon signed rank test, $P < 0.01$, Table 1). However, the proportion of all the adult (AHY) birds that we captured that were forest-interior Neotropical migrant species (35% of 243 adult birds) was significantly lower than Robinson's figure (48% of 236, $\chi^2 = 8.7$, $P < 0.005$). Considered individually, seven of the 10 species had fewer adults captured in 1991–1992 compared to 1985–1986 (Table 1), but this result was not statistically significant (Wilcoxon signed rank test, $P > 0.10$).

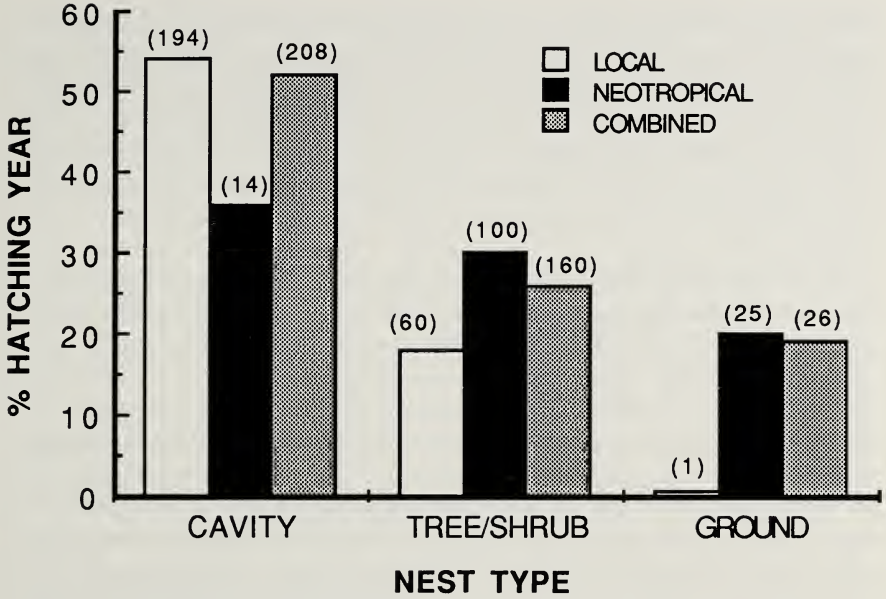

FIG. 1. Percentages of birds caught in mist-net samples in late June through mid-July, 1991–1992 that were hatching year (HY) for three groups of species with different nest types. "Tree/shrub" nesters are species that do not nest on the ground or in cavities. Sample sizes (total caught; HY + AHY) are in parentheses. For local and Neotropical species combined, the HY percentage varied significantly among nest types ($\chi^2 = 31.9$, df = 2, $P < 0.001$).

HY birds made up similar proportions in both 1991–1992 and 1985–1986 when all local species where pooled (45% vs 42% of 264 and 201 individuals, respectively; $\chi^2 = 0.6$, $P > 0.50$). In both studies, the HY proportion was significantly higher for local species than for Neotropical migrants ($P < 0.005$).

Our index of reproductive success varied significantly by nest type ($P < 0.001$, Fig. 1). For all species combined, cavity nesters had the highest proportion of HY birds (52% of 208 in 1991–1992, 44% of 131 in 1985–1986) and ground nesters had the lowest (19% of 26 in 1991–1992, 12% of 33 in 1985–1986). However, within a nest type, the proportion of birds that were HY did not differ between local species and Neotropical migrants (1991–1992 data, $\chi^2 < 2.7$, $P > 0.10$, Fig. 1).

Fewer Brown-headed Cowbirds were caught in 1991–1992 than in 1985–1986. Cowbirds made up 10% of all birds captured in 1985–1986 (N = 324) compared to 2% (N = 383) in 1991–1992 ($\chi^2 = 17.1$, $P < 0.001$). They were the third most abundant species captured in mist-nets in 1985–1986 but only the 16th most abundant species in 1991–1992. Species that

build open cup nests but are known to reject cowbird eggs (i.e., "rejector" species, Rothstein 1975, Appendix I) had a significantly higher percentage of HY individuals among the birds Robinson captured in 1985–1986 (49% of 39) than did all other species combined (22% of 285; $\chi^2 = 12.9$, $P < 0.001$). HY birds made up only 25% of the individuals of rejector species captured in 1991–1992 (8 of 32), a proportion that was marginally lower than that for all other species combined (41% of 371; $\chi^2 = 3.1$, $P < 0.10$).

Return rates of AHY Neotropical migrants between the first and second years of both Robinson's study and ours were similarly low (15% and 19% respectively, $\chi^2 = 0.2$, $P > 0.50$). Return rates for local species were lower (14% in 1991–1992, 7% in 1985–1986).

Results from the few nests and recently-fledged family groups that we observed generally supported our mist-netting data. Only 25% of the open-cup nests (3 of 12) that we found contained eggs or nestlings of cowbirds compared to 67% (49 of 73) for Robinson (1992; $\chi^2 = 7.7$, $P < 0.01$). Of seven recently-fledged family groups of Neotropical migrants observed in 1991–1992 (1 Scarlet Tanager, 1 Red-eyed Vireo, 2 Kentucky Warbler, 2 Ovenbird, 1 Wood Thrush), five had host young only (71%) compared to 33% (7 of 21) for the same species in 1985–1986 (Robinson 1992; Fisher's exact test, $P = 0.10$). Only one of the seven groups (14%) contained only cowbird fledglings (vs 12 of 21 in 1985–1986 [Robinson 1992], Fisher's exact test, $P = 0.06$).

DISCUSSION

Based on the fact that our HY : AHY ratio for forest-interior Neotropical migrants in 1991–1992 was about four times greater than was Robinson's (1992) in 1985–1986, it appears that reproductive success of these species in the Lake Shelbyville area has improved significantly in the past five years. Reproductive success for Neotropical migrants in these forest fragments may not always be as low as it was in 1985–1986. In fact, the HY : AHY ratio for forest-interior Neotropical migrants in 1991 alone was nearly 1.0 (and virtually identical to the HY : AHY ratio for local species that year). Thus, this index of reproductive success has varied nearly an order of magnitude (HY : AHY ratios of 0.1 to 1.0) in the past 5–6 years. An important question is how frequently do these "good years" occur? They may be relatively rare, however, as our HY : AHY ratio for Neotropical migrants dropped back to 0.25 in 1992 (still 2.5 times higher than in 1985–1986).

One explanation for the higher reproductive success of Neotropical migrants in 1991–1992 was the apparent reduction in cowbird parasitism, suggested by four pieces of data. First, we caught a much lower proportion

of cowbirds in our mist-net samples (2% vs 10%) than did Robinson. Second, although we found only 12 nests, the proportion of nests that were parasitized was half that found in nests in 1985–1986. Third, most of the recently-fledged families of Neotropical migrants that we observed contained only host young, in contrast to Robinson's (1992) findings. Finally, rejector species appeared to have higher reproductive success in 1985–1986 but somewhat lower reproductive success in 1991–1992 compared to species that accept cowbird eggs. This suggests that cowbird parasitism may have been an important factor limiting reproductive success for many species of open-cup nesters in 1985–1986 but not in 1991–1992. Why the frequency of cowbird parasitism should have dropped is unclear to us. However, the fact that the relative abundance of all forest-interior Neotropical migrant adults combined (i.e., common cowbird hosts) declined significantly between the studies may be a partial explanation. The precipitous drop (i.e., >50%—Table 1, see also Robinson 1992) in the population size of the Wood Thrush, an especially vulnerable cowbird host, may be particularly significant. However, two other common cowbird hosts (Red-eyed Vireo and Scarlet Tanager) appeared to have increased since 1985–1986.

Despite the fact that reproductive success appeared to be over three times higher for forest-interior Neotropical migrants during our study, overall productivity for these species was still low. Only 29% of the Neotropical migrants we captured were fledglings (HY) compared to 45% for all local species, 54% for cavity-nesting local species in general, and 67% for the Tufted Titmouse (51 of 76) in particular. High levels of nest predation appeared to be the primary cause of this low reproductive success during our study. Cavity-nesting species, less vulnerable to predation than open-nesting species (Ricklefs 1969), had significantly higher proportions of HY birds than did non-cavity nesting species (52% vs 25%), for all species combined (Neotropical + local). Ground-nesting species, probably the most vulnerable to mammalian predators, had the lowest proportion of HY birds (19%) despite the fact that these species should be the most likely to be captured in our mist nets. Thus, the higher reproductive success for local species largely reflects the preponderance of cavity-nesting species in this group (and the near lack of ground-nesting species) compared to the Neotropical migrants. Artificial nest studies (Linder 1992, Bollinger, unpubl. data) in our study area also indicate very high levels of nest predation, primarily due to mammals such as raccoons (*Procyon lotor*). Over 90% of the artificial nests that we placed in these woodlots were disturbed by predators within six days.

Whereas cowbird parasitism may have abated somewhat in the 5–6 years since Robinson's study, high levels of nest predation, especially on

open-nesting species, continue. Robinson's (1988, 1992) conclusion that these woodlots represent population sinks for Neotropical migrants still appears to be correct. However, these sinks may not be quite as "deep" as originally proposed. Long-term studies are necessary to determine how frequently good reproductive years for Neotropical migrants occur in this fragmented forest.

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Appendix I

Classification of Birds Captured in Mist Nets in Forest Fragments Adjacent to Lake Shelbyville, Illinois According to Migratory Status

Species	Migration[a]	Habitat[b]	Nest type
Northern Bobwhite (*Colinus virginianus*)	L	—	G
Yellow-billed Cuckoo (*Coccyzus americanus*)	N	I	T/S
Ruby-throated Hummingbird (*Archilochus colubris*)	N	E	T/S
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	L	—	C
Red-bellied Woodpecker (*Melanerpes carolinus*)	L	—	C
Downy Woodpecker (*Picoides pubescens*)	L	—	C
Hairy Woodpecker (*Picoides villosus*)	L	—	C
Northern Flicker (*Colaptes auratus*)	L	—	C
Eastern Wood-Pewee (*Contopus virens*)	N	I	T/S
Acadian Flycatcher (*Empidonax virescens*)	N	I	T/S
Great Crested Flycatcher (*Myiarchus crinitus*)	N	I	C
Blue Jay* (*Cyanocitta cristata*)	L	—	T/S
Black-capped Chickadee (*Parus atricapillus*)	L	—	C
Tufted Titmouse (*P. bicolor*)	L	—	C
White-breasted Nuthatch (*Sitta carolinensis*)	L	—	C
Carolina Wren (*Thryothorus ludovicianus*)	L	—	C
Blue-gray Gnatcatcher (*Polioptila caerulea*)	N	E	T/S
Eastern Bluebird (*Sialia sialis*)	L	—	C
Wood Thrush (*Hylocichla mustelina*)	N	I	T/S
Gray Catbird* (*Dumetella carolinensis*)	L	—	T/S
Brown Thrasher* (*Toxostoma rufum*)	L	—	T/S
Red-eyed Vireo (*Vireo olivaceus*)	N	—	T/S
Prothonotary Warbler (*Protonotaria citrea*)	N	E	C
Worm-eating Warbler (*Helmintheros vermivorus*)	N	I	G
Ovenbird (*Seiurus aurocapillus*)	N	I	G
Louisiana Waterthrush (*S. motacilla*)	N	I	G
Kentucky Warbler (*Oporornis formosus*)	N	I	G
Summer Tanager (*Piranga rubra*)	N	E	T/S
Scarlet Tanager (*P. olivacea*)	N	I	T/S
Northern Cardinal (*Cardinalis cardinalis*)	L	—	T/S
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	N	E	T/S
Indigo Bunting (*Passerina cyanea*)	N	E	T/S
Common Grackle (*Quiscalus quiscula*)	L	—	T/S
Brown-headed Cowbird (*Molothrus ater*)	L	—	—
Northern Oriole* (*Icterus galbula*)	N	E	T/S
American Goldfinch (*Carduelis tristis*)	L	—	T/S

[a] Migration status, habitat type, and nest types: L (local)—included both residents and short-distance migrants; N (Neotropical migrant); I, (forest interior); E (forest edge); C (cavity); G (ground); T/S (tree/shrub). Species with an asterisk are known to reject cowbird eggs.

[b] Local species were not classified according to habitat. Neotropical migrants classified as "interior and edge" species by Whitcomb et al. (1981) and Freemark and Collins (1992) are here listed as either "interior" or "edge" for comparison with Robinson (1992).

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NOCTURNAL FLIGHT CALL OF BICKNELL'S THRUSH

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ABSTRACT.—Audio recordings of nocturnal flight calls of migrating birds along the east-central Florida coast in May have documented calls that sound similar to those from Gray-cheeked Thrushes (*Catharus minimus*). Spectrographic comparison of these "Florida gray-cheeked" calls with Gray-cheeked Thrush calls recorded from Minnesota, southern Alabama, and west-central New York State shows that the Florida calls have distinctive acoustic features. Speculation that the "Florida gray-cheeked" calls are from the Gray-cheeked subspecies (*C. m. bicknelli*), now proposed as a separate species, Bicknell's Thrush (*C. bicknelli*), is supported by spectrographic comparison with a diurnal Bicknell's Thrush call and the coincidence of time and location of the "Florida gray-cheeked" recordings with the known timing and migration route of Bicknell's Thrush. *Received 21 Dec. 1992, accepted 6 May 1993.*

Since Ball's (1952) description of the nocturnal flight call (nf-call) of the Gray-cheeked Thrush (*Catharus minimus*), no progress in identifying the nf-calls of migrating passerines has been reported. However, nearly every fall migration summary in the "Audubon Field Notes" since the late 1950s contains one or more accounts of flight calls heard at night. This paper presents analyses of such calls.

METHODS

Audio recordings were made on evenings when steady calling occurred throughout the following passerine migration seasons in the regions indicated; Minnesota (spring and fall 1987), southern Alabama (Oct. 1989 and spring 1990), west-central New York State (spring 1988 and fall 1988–1991), and east-central Florida (spring 1989 and 1991). The majority of these recordings, and those pertinent to this paper, were made with a Sennheiser 816T "shotgun" microphone with zeppelin windshield, a Shure FP-11 microphone pre-amp, and a Sony TCD-D10 digital audio recorder. A call-type's presence or absence in a region was associated with known migrants for that area. Similarly, associations between call-types and species were deduced by comparing the dates when call-types were recorded with migration timing derived from historic diurnal observations in each region. In many cases, identification of an nf-call was supported by comparing it with a recording of an analogous diurnal call made by a visually-identified bird.

In the spring of 1989, audio recordings of nocturnal flight calls of migrating birds were made at Merritt Island National Wildlife Refuge (MINWR), 5 km east of Titusville, Brevard County, Florida. The recording effort began on 31 March and continued every evening through 6–7 May. In the early morning of 6 May, two nf-calls were recorded that sounded like those given by the Gray-cheeked Thrush, yet seemed to be different from Gray-cheeked nf-calls that had been recorded from other regions of North America. Because only two of these unusual calls were obtained, and it was known that *Catharus* thrushes have a fair amount of variation in their calls (Ball 1952), this impression lay dormant.

In the spring of 1991, audio recordings of nf-calls were again made in peninsular Florida.

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During the period 13–16 May, nf-calls were recorded from the Canaveral National Seashore north headquarters, 16 km southeast of New Smyrna, Brevard County, Florida. This location is approximately 30 km north of the MINWR location where recordings were made in 1989 and is approximately 100 m from the Atlantic Ocean. Over 10,000 nf-calls were documented during these three nights (8 hours of recording per night). Among these calls were 28, from an estimated 17 birds, believed to be those of Gray-cheeked Thrushes. Again, however, the aural distinctiveness that was noticed in 1989 was heard. Now, with a larger sample size, a consistent difference in the "gray-cheeked" nf-calls recorded in spring migration from east-central Florida was noted.

In looking for an explanation for the uniqueness and limited geographic distribution of the "Florida gray-cheeked" nf-calls, their resemblance to the nf-call of the Gray-cheeked Thrush led to the suspicion that they might be from a different Gray-cheeked subspecies. Range considerations directed the investigation toward the subspecies *C. m. Bicknelli* which has recently been proposed as a separate species, Bicknell's Thrush (*C. bicknelli*) (Ouellet, 1993). Bicknell's Thrush breeds in northeastern North America along the southern part of the north shore of the Gulf of St. Lawrence, in the mountains of the Gaspé Peninsula, and in the mountains of the northeastern United States. Its only known wintering ground is the mountainous islands of the Caribbean, primarily Hispaniola (Ouellet 1993). Migration records indicate that it uses the Atlantic coastal plain in transit between breeding and wintering grounds (Wallace 1939, Ouellet 1993).

The absence of the "Florida gray-cheeked" call-type in the author's extensive recordings in fall migration from southern Alabama, Minnesota, and west-central New York State (Ithaca and Alfred areas) coincides with the fact that these locations are outside of the known fall migration route of Bicknell's Thrush. Three Bicknell's Thrush specimens have been collected in east-central Florida in spring (Wallace 1939) indicating that some portion of their population migrates through the region where the "Florida Gray-cheeked Thrush" nf-calls were recorded.

To support the Bicknell's Thrush possibility, spectrographic analyses of nf-calls were performed at the Cornell Laboratory of Ornithology in the Bioacoustics Research Program. Recordings of all calls were converted into digital files using a "Macrecorder" analog-to-digital converter at a sampling rate of 22254 Hz. Spectrographic analysis was performed using the "Canary 1.0" software developed by the Cornell Laboratory of Ornithology's Bioacoustics Research Program. Spectrographs of the digitized calls were made using a 512 pt FFT, 128 point frame size, 90% overlap, and Hanning window (frequency resolution = 21.7 Hz; time resolution = 5.75 msec; analysis bandwidth = 713 Hz).

RESULTS

Gray-cheeked Thrush nf-calls were selected from each of the regions where extensive recording had been conducted (Minnesota, southern Alabama, and west-central New York) for comparison with the "Florida gray-cheeked" nf-calls. The number of nf-calls chosen from each region was limited to the number of calls of suitable amplitude for spectrographic analysis that were available. In cases where several loud calls seemed to be given by the same bird, only one of these nf-calls was used. Due to the altitude at which birds were often flying, most recordings were of insufficient amplitude to illustrate spectrographically the full contour of the call. For example, in Florida, while 30 "gray-cheeked" nf-calls were

recorded from an estimated 19 individual birds, nf-calls from only eight birds were of sufficient amplitude. From the other regions, though hundreds of Gray-cheeked nf-calls were recorded, only nine were suitable from southern Alabama, 17 from Minnesota, and eight from west-central New York State. In addition to the nf-calls, diurnal calls from Bicknell's and Gray-cheeked thrushes from Cornell Laboratory of Ornithology's Library of Natural Sounds (LNS) were spectrographically analyzed to see if diurnal calls of each species could be found that might help corroborate the nf-call identities.

The dominant structure of the eight "Florida gray-cheeked" nf-calls is a tone with a bandwidth of 0.5–1.0 kHz and a duration of 150–280 msec (Fig. 1A). The tone's time-frequency contour varies from an initial frequency of 1.5–2.0 kHz, through a rather steep ascent, so that within 10–20 msecs, a frequency of 4.8–5.8 kHz is attained. From this point, the tone's frequency descends at a fairly uniform rate of between 6–8 Hz per msec. This uniform descent characterizes the greater portion of these nf-calls, and in at least the latter half of each call, a modulation frequency of between 120–150 Hz is evident. The initial rising section has a lower amplitude than the uniformly descending portion of the calls. Spectrographs of weakly recorded nf-calls lacked the initial rising section and showed only the uniformly descending structure.

The Gray-cheeked nf-calls from west-central New York State, southern Alabama, and Minnesota show relatively little variation between recording locations. These nf-calls are similar to the Florida Gray-cheeked Thrush nf-calls in their duration, bandwidth, and modulation frequency, but their time-frequency contours are distinctly different. Table 1 illustrates this by comparing the average frequency of certain common structural features in the nf-calls. The first frequency measurement point is at the highest frequency of the first "bend" in each call, a bend being a distinctive inflection in the slope of the call's time-frequency contour. The second frequency measurement point is the highest frequency that is greater than the first point in the call. In the case of the Florida Gray-cheeked Thrush nf-calls, there was no second frequency measurement since the first point was always the highest frequency in the call. The third frequency measurement point is the frequency at the end of the call.

The basic statistics for the frequency measures of the Gray-cheeked and Florida Gray-cheeked Thrush nf-calls demonstrate that these two groups of nf-calls are not similar (Table 1). The frequency of the first inflection point in the Gray-cheeked nf-calls averages more than 1 kHz lower than the first inflection in the "Florida gray-cheeked" nf-calls. Furthermore, the Gray-cheeked nf-calls average nearly 1 kHz lower than the "Florida gray-cheeked" nf-calls at the frequency where the call terminates.

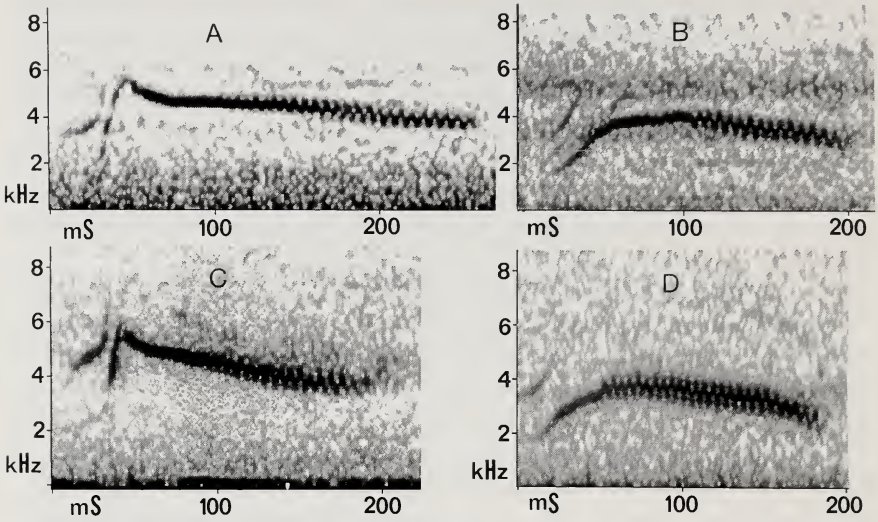

FIG. 1. Spectrograms of calls. Y-axis represents frequency in kilohertz (kHz). X-axis represents time in milliseconds (mS). (A) is a "Florida gray-cheeked" nf-call. (B) is a Gray-cheeked Thrush nf-call. (C) is a Bicknell's Thrush diurnal call. (D) is a Gray-cheeked Thrush diurnal call.

Besides the frequency domain differences, the two nf-call groups have characteristic shapes. The Gray-cheeked nf-calls have an arched (variably sloped) descent after the first inflection, while the "Florida gray-cheekeds" have a uniformly descending slope (Figs. 1A and 1B).

Another distinction, which aided in detecting the uniqueness of the "Florida gray-cheeked Thrush" nf-calls in the field, is that the modulation amplitude in the latter part of these calls averages 25–50% lower than in Gray-cheeked Thrushes. This makes the "Florida gray-cheeked Thrush" nf-call sound notably more pure-toned.

The Cornell Library of Natural Sounds contains several recordings of diurnal calls from each of these species. Among these recordings, an example of a diurnal call from a Gray-cheeked Thrush was found (Fig. 1D) that has frequency domain and shape parameters that match those of the Gray-cheeked nf-calls. This recording (LNS #4202) was made by A. A. Allen and P. P. Kellogg on 4 July 1954 at Churchill, Manitoba. It shows the characteristic "arched" shape of the Gray-cheeked nf-calls, and its highest frequency point (4.0 kHz) and ending frequency point (2.8 kHz) are also concordant.

Among the Bicknell's Thrush recordings at LNS, a diurnal call was found (Fig. 1C) that has frequency domain and shape parameters that

TABLE 1
AVERAGE FREQUENCIES (KHZ) OF COMMON STRUCTURAL POINTS IN THE NF-CALLS FROM EACH REGION

Location	Frequency points[a]		
	1	2	3
New York State (8 nf-calls)	3.6 (0.21)	4.0 (0.15)	2.5 (0.19)
Minnesota (17 nf-calls)	3.6 (0.25)	4.2 (0.18)	2.8 (0.33)
Alabama (9 nf-calls)	3.9 (0.10)	4.1 (0.11)	2.8 (0.21)
Florida (8 nf-calls)	5.3 (0.29)	—	3.7 (0.29)

[a] SD in parentheses.

match those of the "Florida gray-cheeked" nf-calls. This recording (LNS #4208) was made at Mount Mansfield, Vermont, on 29 June 1953, also by Allen and Kellogg. It has both the initial high frequency peak (5.7 kHz) and high ending frequency (3.8 kHz) characteristic of the "Florida gray-cheeked" nf-calls as well as the uniformly descending similarity.

Furthermore, although just a few diurnal recordings of each species were available, no diurnal Gray-cheeked calls had frequency domain and shape parameters that matched those of the Bicknell's nf-calls. Similarly, no Bicknell's diurnal calls were found that had frequency and shape parameters matching those of the Gray-cheeked nf-calls.

DISCUSSION

Range considerations strongly favor the Manitoba diurnal Gray-cheeked call as well as the Minnesota Gray-cheeked nf-calls to be from the subspecies *C. m. aliciae* (Wallace 1939, Ouellet, 1993). The similarity of the Gray-cheeked nf-call subsets from New York and Alabama to the one from Minnesota, as indicated in Table 1, suggests that these nf-calls could also be from *C. m. aliciae*. Nf-calls from the subspecies *C. m. minima* could be involved if they are similar to those of *C. m. aliciae*; however, nothing is currently known about their nf-calls. It is intriguing that a large sample of nf-calls from east-central Florida during the spring migration period of the Gray-cheeked Thrush did not yield a single "*aliciae*-type" Gray-cheeked Thrush nf-call.

Range considerations have been mentioned which make Bicknell's Thrush a likely migrant in east-central Florida. Also, the time of year that the "Florida gray-cheeked" calls were recorded compares favorably with Bicknell's known migration timing based on collected specimens. An overview of the relatively few specimen records that exist show that the dates they were collected are coincident with the timing of the "Florida

gray-cheeked" nf-calls. Wallace (1939) lists eight specimens that are unquestionably Bicknell's Thrush taken from Florida to North Carolina between 3–18 May. Sight records of ten Gray-cheeked Thrushes (not identified as to subspecies) in Brevard County, Florida, with dates ranging from 6 May to 22 May have been reported (Cruickshank 1986). No published records were found that contradict the possibility, based on migration timing, of the "Florida gray-cheeked" nf-calls being those of Bicknell's.

It is evident from reading Ball's (1952) work that he speculated on, and even had a strong hunch about, the nf-call of Bicknell's Thrush. The phonetics he used to describe the nf-calls he heard in late September of 1948, that he speculated might be from Bicknell's Thrush, were "cree-e-e" (Ball 1952:52). This is different from phonetics like "pe-i-i-i-r", "cheerrr", and "whe-errr" that he, and others, have used to describe the nf-call of the Gray-cheeked Thrush. Three types of phonemes are usually used to represent Gray-cheeked's nf-call. Because the high frequency point is near the middle of the call, the initial lower frequency part of the call is perceived and this, in turn, helps distinguish the higher frequency in the center of the call. Because of the ensuing frequency drop from the middle to the end of the call, the call is perceived to change in pitch from low to high to low, and this pattern is represented most accurately by three types of phonemes.

With the "Florida gray-cheeked" nf-calls, the characteristic abrupt frequency rise at the beginning of the call is so fast and of relatively weak amplitude that it is not easily distinguished by the human ear. The call sounds as if it changes in pitch from high to low, with the bulk of its duration a mild, uniform descent which is characterized best by repeating one type of phoneme. Since no phoneme is needed to represent an initial lower frequency part of the call, only two types of phonemes are needed, and there is no need for an "r" at the end of this nf-call's phonetic representation. Indeed, Ball's "Cree-e-e" fits the "Florida gray-cheeked" nf-calls well.

Ball tried to distinguish the nf-call of Bicknell's Thrush in a region where both Bicknell's and Gray-cheeked Thrush were migrants. His respect for potential variations in thrush nf-calls made certainty in the identity of Bicknell's nf-call difficult to obtain. The author was aided in abstracting nf-calls believed to be from Bicknell's Thrush by having learned and sampled the variations of the nf-call of Gray-cheeked Thrush in Minnesota, where Bicknell's Thrush is not a migrant. This allowed the pure sample of higher pitched and more pure-toned "gray-cheeked" nf-calls from east-central Florida to stand out.

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COMMUNAL ROOSTING AND FORAGING BEHAVIOR OF STAGING SANDHILL CRANES

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ABSTRACT.—Each spring more than 300,000 Sandhill Cranes (*Grus canadensis*) roost communally at night in river channels in the Platte River Valley of Nebraska and disperse at dawn to forage in agricultural fields. Cranes with central roosts had activity ranges double the size of those with peripheral roosts; 42% of the birds changed activity ranges prior to the onset of migration. Minimum daily flight distance generally increased during the staging period. Cranes used native grassland and planted hayland more often than expected, relative to their percentage of occurrence, and fed longest there; cornfields were under-utilized. These differences probably reflect, in part, (1) limited distribution of grasslands and haylands resulting in a greater energy expenditure to acquire protein in the form of macroinvertebrates and (2) wider distribution of cornfields with adequate energy-rich foods but limited protein. Cranes probably forage more efficiently and conserve energy by following conspecifics from communal roosts to local feeding grounds, by settling in fields where foraging flocks are already present, and by establishing diurnal activity centers. Alert behavior varied with flock size but not as predicted from group size, presumably because predation of staging adult cranes is inconsequential. *Received 4 Jan. 1993, accepted 15 June 1993.*

Sandhill Cranes of the midcontinent population acquire nutrient reserves for migration and reproduction while on staging areas along the Platte and North Platte rivers in Nebraska (Krapu et al. 1985). Cranes roost communally at night in shallow waters of wide river channels or other wetlands and spend the days foraging in flocks on surrounding uplands (Krapu et al. 1984, Folk and Tacha 1990). Little is known concerning the specific functions of communal roosting and flocking to staging cranes beyond a probable advantage of reducing the risk of predation through increased predator detection (sensu Pulliam 1973, Caraco 1979) or evasive behaviors unique to groups. In some species of birds, communal roosts may serve as information centers, increasing foraging efficiency (Ward and Zahavi 1973; Waltz 1982, 1987; but see Bayer 1982; Stutchbury 1988 for contrary opinions). Foraging efficiency can also be increased through local enhancement (Hinde 1961) or use of alternative diurnal roosts (Caccamise and Morrision 1986, 1988).

In the Platte River Valley, loss of communal roosting habitat has resulted in high densities of staging cranes (Krapu et al. 1984) prompting a need to evaluate spatiotemporal use of existing habitat and choice of foraging sites. In this paper, we examine (1) characteristics and use of

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activity ranges relative to energy expenditure and food availability, (2) the role of communal roosts in foraging behavior, (3) habitat preferences, and (4) influence of group size and predation on foraging and other behaviors. We also discuss social factors as they pertain to staging behavior in Sandhill Cranes.

STUDY AREA AND METHODS

The study area encompassed 253-km^2 along the Platte River between Kearney and Shelton, Nebraska. Habitat composition within the study area was 49.8% cornfields, 17.3% native grassland, 10.8% planted hayland (primarily alfalfa and planted grasses), 11.6% riverine, and 10.5% other (roads, homesteads, plowed fields). Interstate 80 (I-80) is adjacent to the north channel of the Platte River. A more complete description is in Krapu et al. (1984).

Radiotelemetry.—During March and April 1978 and 1979, cranes were live-trapped with rocket and cannon-projected nets positioned near groups of mounted crane decoys in cropland and pastures. To minimize disturbance, nets were fired from blinds located several hundred m from decoys. Each captured bird was weighed, aged as juvenile or adult by head plumage (Lewis 1979), and banded. Battery-operated transmitters weighing approximately 40 g (<2% of body weight) were attached to 13 cranes in 1978 and 23 in 1979, using a neck and body loop and backpack harness. Ten birds in 1978 (8 adult, 2 juvenile) and 14 in 1979 (13 adult, one juvenile) were located frequently enough to permit statistically valid analyses of activity ranges and movements.

When feasible, each radio-equipped crane was located at hourly intervals during daylight and once each just after dusk and before dawn. Locations were determined by triangulation from ground vehicles to the nearest 100 m. Fixed-wing aircraft were used when birds could not be located from the ground. No individual was followed in more than one year.

Distances and angles between locations were calculated along straight lines. These distances represent minimal distances because cranes meandered between radio fixes. Birds that were located in the same habitat on two sequential observations were assumed to have remained in that habitat for the interval, and those located in different sites were assumed to have visited only those in which they were recorded.

Cranes center their activities within definable, undefended areas that may change in size and location through time. These "activity ranges" differ from conventional home ranges in that they are transient and occupied only for roosting and feeding. Areas of activity ranges were estimated with a harmonic means method (Dixon and Chapman 1980) including the 95% closest points. When cranes used two or more discrete (as determined by non-overlapping clusters of locations separated by at least 2 km) activity ranges, separate areas were calculated for each.

Time budgets.—Diurnal time budgets were developed within each of the habitats by recording activities of individual cranes at 12-sec intervals throughout the staging period. Time spent observing in each habitat was proportional to the percent of study area covered by that habitat. Individuals were selected arbitrarily by locating a group of cranes in a spotting scope's field of view and, after looking away and slightly moving the scope horizontally and vertically, observing the individual nearest to the intersection of the cross hairs. Observations on an individual lasted from a few sec to 5 min. Observations occurred from 06:00 to approximately 18:00 h CST. Behavioral categories included "resting" (sitting or standing still), "feeding", "alert", "calling", "courting", "aggression" (fighting or being attacked), "locomotion" (walking), and "comfort" (preening). An "unknown" category contained observations that could not be classified as one of the other behaviors.

Statistical analyses.—Unless otherwise stated, all values are means ± SD. Statistical treatment of distances flown, either among habitats or within a day, were complicated both by missing cells in some cases and repeated observations from marked individuals. We used repeated-measures analysis of variance (Milliken and Johnson 1984) on these data. Angular statistics and correlations were conducted following Batschelet (1981). Behavioral frequencies based on counts were analyzed with *G*-tests (Sokal and Rohlf 1969). Sequential behaviors may not have been truly independent, but we believe that observations were adequately dispersed over birds, groups, and contexts to warrant this type of statistical treatment.

RESULTS

Characteristics and use of activity ranges.—Fifty-seven percent of the nocturnal roosts were centrally located within the activity ranges, 37% were at the periphery, and 6% had too few observations to determine type of activity range (Table 1, Fig. 1). Fourteen birds maintained one activity range, nine had two distinct activity ranges (crane 78–10 had two ranges but only one with enough observations for statistical purposes), and one had three ranges. Among cranes with peripheral roosts, 73% had activity ranges south of their nocturnal roosts.

We tested whether activity range size was dependent on type of roost, year, or interaction between type and year. Because accuracy of estimating activity range size is related to the number of observations for an activity range, we weighted the analysis by multiplying the squared residual for each observation by the square root of the number of observations within each range (SAS 1987). Size of activity range differed between roost types ($P = 0.049$). The weighted mean activity range area for individuals with central roosts (39.6 ± 64.3 km^2) exceeded that of peripheral roosts (17.4 ± 29.0 km^2). The unweighted mean for central roosts was 38.7 ± 17.1 km^2 and for peripheral roosts was 17.4 ± 8.3 km^2. There were no differences between years or in interaction between roost type and year ($P > 0.11$).

To test whether the type of roost affected travel distances to foraging locations, we compared the means of distances for first flights in the morning from roosts to feeding locations between years and type of roost. If a crane had two activity ranges of the same type, a combined mean was obtained by weighting each separate mean by its sample size. Means of actual distances from roosts to initial feeding areas did not differ between activity ranges with peripheral roosts (1285 ± 388 m) and those with central roosts (1408 ± 407 m) nor between years or interaction between years and roost type ($P > 0.40$).

We also examined changes in activity range size and in daily travel distance through the staging period. Activity range types were pooled to assure adequate sample size. No differences were noted between years, among weeks, or in the interaction of the two terms ($P > 0.26$).

TABLE 1

NUMBER, TYPE, AND SIZE (KM²) OF ACTIVITY RANGES OF SANDHILL CRANES DURING STAGING AT THE PLATTE RIVER, NEBRASKA

Year	Bird	Number of ranges	Activity range size (days observed)	
			Central	Peripheral
1978	1	1	15.3 (16)	
	3	2	30.3 (8), 23.0 (12)	
	4	2	47.1 (18)	8.9 (8)
	5	1		15.9 (19)
	6	1		23.6 (3)
	10	2[a]		15.8 (4)
	12	1	15.3 (16)	
	13	1[b]		
	15	1		17.6 (20)
	16	1		11.8 (20)
1979	2	1	30.5 (35)	
	3	2	70.5 (26), 5.9 (9)	
	4	1	37.4 (29)	
	5	1	61.4 (30)	
	10	1	44.2 (25)	
	11	2		2.5 (2), 6.0 (6)
	12	2	44.6 (21), 34.5 (8)	
	13	3	25.3 (3)	10.2 (8), 12.6 (21)
	14	2	32.1 (13)	23.5 (2)
	15	2	49.6 (9)	17.5 (6)
	16	1	80.3 (27)	
	17	1	41.1 (18)	
	18	1		37.4 (22)
	19	2	21.2 (22), 4.9 (6)	

[a] Only one activity range had sufficient observations to estimate size and determine type.
[b] Insufficient observations to estimate size or type.

Minimum daily flight distance varied among weeks ($P = 0.019$). In 1978, flight distances increased from the first to the third week and then declined. In 1979, the increase lasted through the fourth week (Fig. 2). Minimum daily distance was also greater in 1979 (7858 ± 3950 m) than in 1978 (5705 ± 3577 m) ($P = 0.023$). None of the interactions between weeks, years, or roost type was significant ($P > 0.14$).

Information sharing and associations among roosting cranes.—We looked at two major sources of data to determine if cranes followed each other to specific foraging sites. First, we examined synchrony of departure from nocturnal roosts to feeding sites. Synchrony could mean that birds follow each other or that they use a common extrinsic stimulus such as

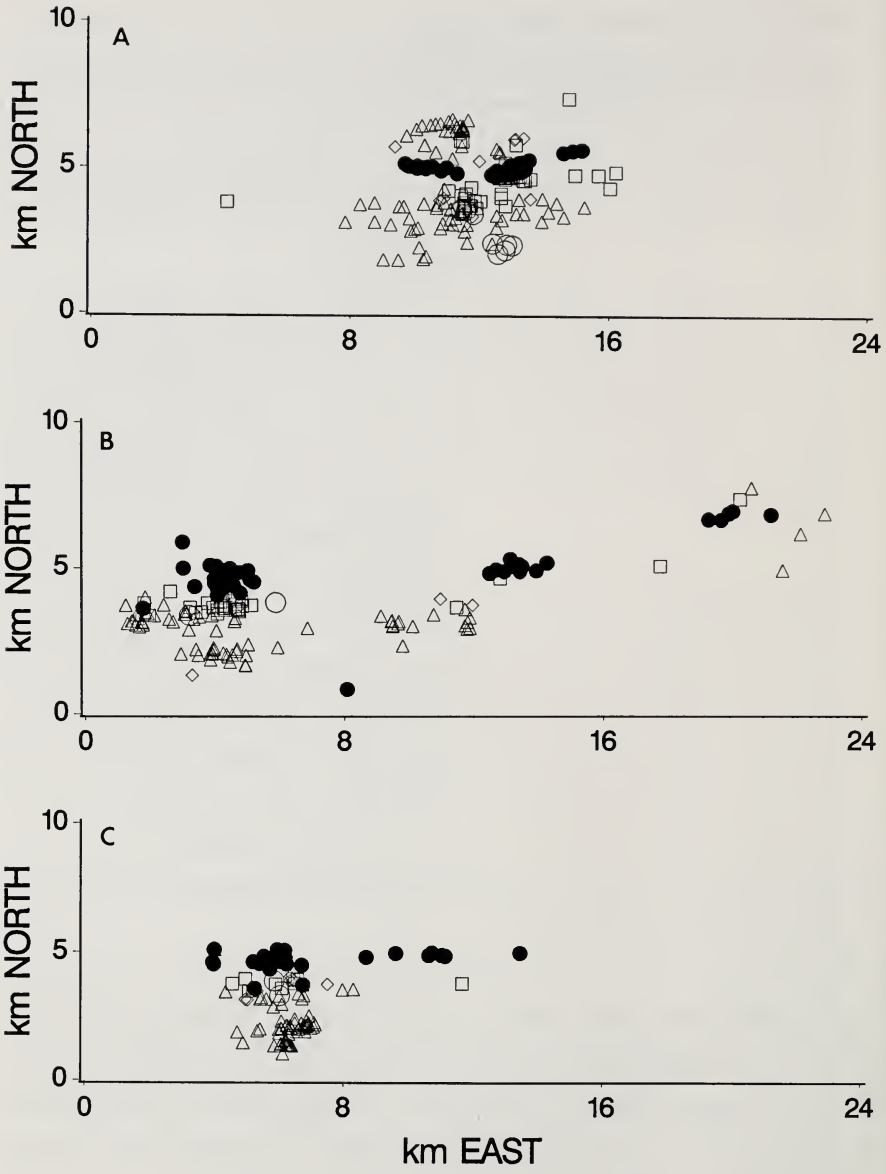

FIG. 1. Examples of activity ranges and habitat locations for staging Sandhill Cranes. A. Bird 79-2 with a centrally located roost, B. Bird 79-13 with three discrete activity ranges, two of which have peripheral roosts, C. Bird 79-18 with a peripheral roost. Habitat types are riparian—closed circles; native grassland—squares; planted hayland—diamonds; cornfields—triangles; other—open circles. Coordinates are based on a common meridian in the universal transverse mercator system. Approximately 33% of all observations were randomly deleted to improve clarity of figures.

sunrise to time departures. We used a χ^2 goodness-of-fit test to compare data presented by Lewis (1974) on crane departures to a Poisson distribution (Fig. 3). Lewis' data indicated that crane departures were more clustered than would be expected by chance ($P < 0.0001$).

Second, we noted that most telemetry locations occurred south of the roosts, suggesting a tendency for roost mates to flock together. For example, five of seven cranes in 1978 with sufficient observations and 12 of 13 in 1979 left roosts in a southern direction. Seventy-five percent of 3102 telemetry locations were south of the communal roosts. The frequency of telemetry locations to the south was higher for peripheral roosts (90.3%) than for central roosts (66.2%) ($P = 0.0035$), for 1979 (78.1%) than for 1978 (70.4%) ($P < 0.0001$), and for interaction between year and type of roost ($P < 0.0001$) (PROC CATMOD, SAS 1987). In 1979, peripheral roosts had a higher percentage of locations south of the communal roosts relative to central roosts than in 1978.

To address further whether cranes from the same roost flew to identical feeding areas, we correlated the angles of morning departures from roosts among all birds. In 1978, only three of 16 possible correlations proved significant ($P < 0.05$). In 1979, relationships were even weaker with three of 69 possible correlations significant ($P < 0.05$). The number of significant correlations in 1979 was not greater than would be expected by chance based on our accepted value for significance.

Habitat preferences.—Usage relative to availability gives some indication of preferred habitats. We characterized activity ranges used by six cranes in 1978 and 14 in 1979. Average habitat composition of these ranges was 44.3% cornfields (range 35.7–51.0%), 19.7% native grassland (12.6–25.8%), 9.6% planted haylands (7.1–14.2%), 17.9% riverine (7.6–29.2%), and 8.5% other (3.4–20.3%). We used the method of Byers et al. (1984) to compare number of locations within each habitat with availability based on overall habitat composition in the study area (Table 2). There was a highly significant difference ($P < 0.0001$) between use and availability. Sandhill Cranes used riverine habitats, native grasslands, and planted haylands more often than expected and cornfields and other habitats less than expected.

Habitat usage varied throughout the day. Before 08:00 h and after 20:00 h 53.1% of the telemetry locations occurred in riverine habitats. Between 08:00–18:00 h cranes primarily used cornfields (51.6% of all locations during this period), native grasslands (28.0%) and planted haylands (16.3%). Use of native grasslands (35.6%) and planted haylands (17.5%) increased from 10:00–16:00 h as cranes gathered in traditional resting areas; cornfield use (43.7%) declined during this period. Use of cornfields increased late in the afternoon (56.2%) before cranes returned to nocturnal roosts.

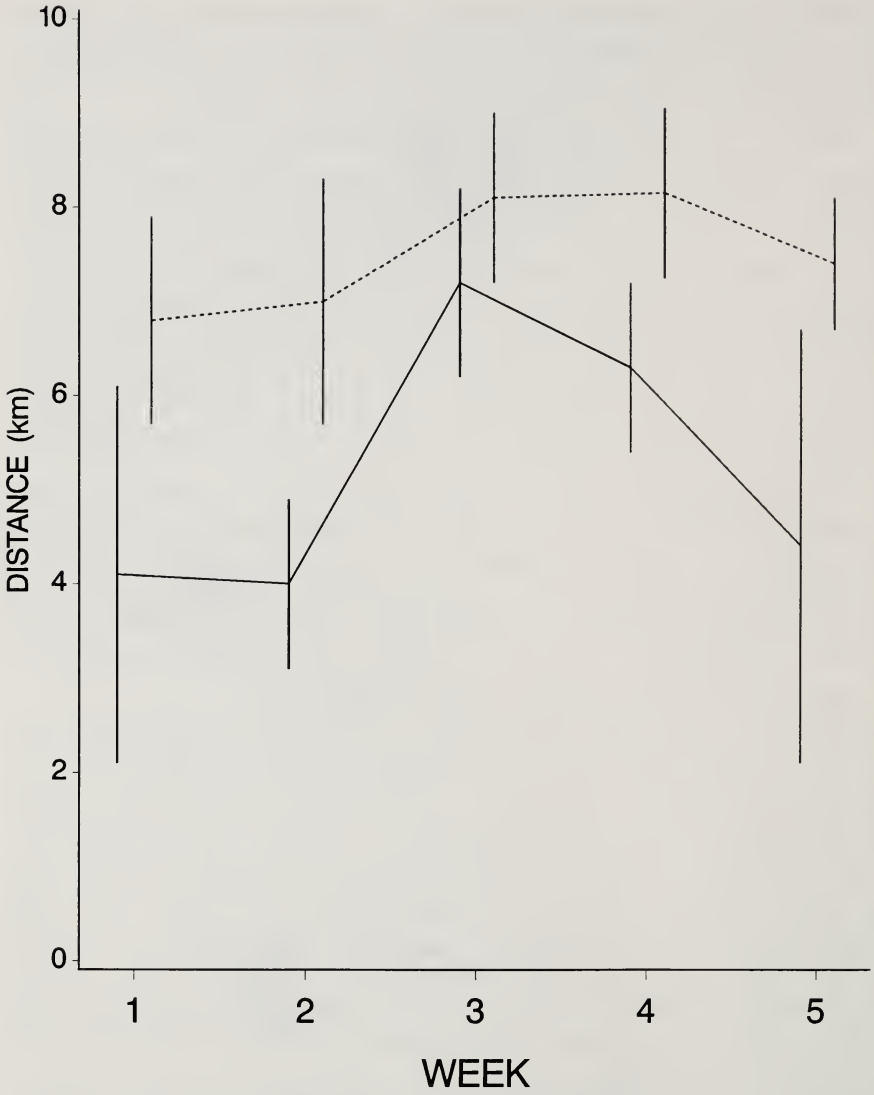

FIG. 2. Minimum daily flight distance through the Sandhill Crane staging periods of 1978 (solid line) and 1979 (dashed line). Birds with peripheral and central roosts are combined within each year. Bars represent $\bar{x} \pm 2$ SE.

We tested whether average flight distance differed among habitats, years, or interaction between year and habitat. To simplify interpretation, we included only cranes that had flown to all five habitats at least once (N = 19) and ignored any effect due to type of activity range. Flight distance

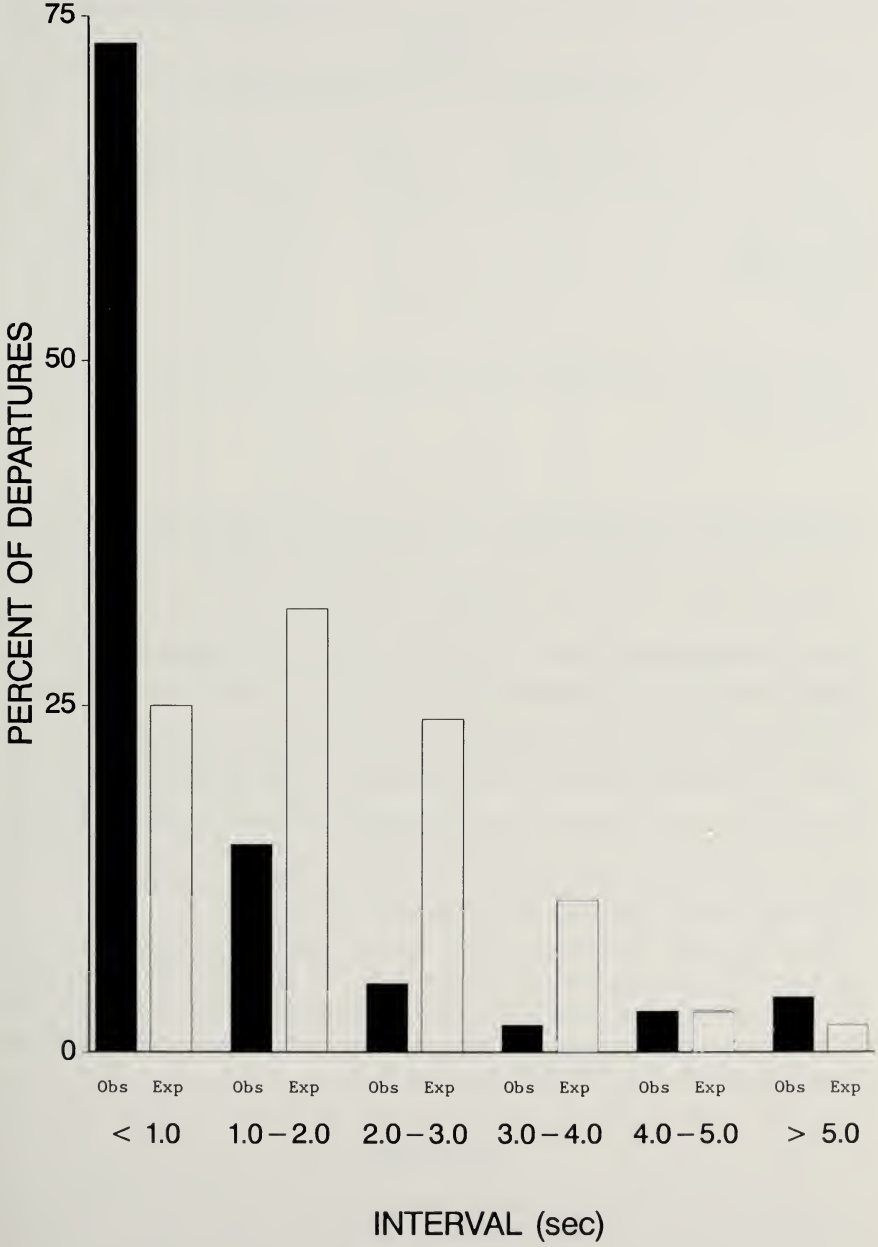

FIG. 3. Observed (filled) frequencies for departure intervals of Sandhill Cranes leaving roost sites compared to expected (open) based on a Poisson distribution of observed values. Data are from Lewis (1974), N = 5850 observations.

TABLE 2
PROPORTION OF SANDHILL CRANE VISITS AND MEAN FLIGHT DISTANCES (M) TO DIFFERENT HABITATS DURING STAGING IN NEBRASKA[a]

Habitat	Percentage of locations		Bonferonni intervals[b]	Flight distance (SD)	
	Observed	Expected		1978	1979
Riverine	26.4	11.6	23.4–29.8	1839 (1137)	2053 (1467)
Native grassland	24.3	17.3	21.0–27.6	1162 (901)	1645 (1321)
Planted hayland	14.8	10.8	12.1–17.5	976 (893)	1440 (1268)
Cornfield	31.7	49.8	30.5–32.9	916 (800)	1589 (1251)
Other	2.8	10.5	2.4–3.2	712 (620)	1286 (755)

[a] A total of 1506 observations were used in the analysis; χ^2 for overall analysis = 531, df = 4, $P < 0.0001$.
[b] If expected values fall outside of Bonferonni interval, the difference between observed and expected is significant at $P \leq 0.05$ (Byers et al. 1984).

depended upon destination ($P < 0.0001$) (Table 2) and year ($P = 0.003$) but not on the interaction between year and habitat ($P > 0.38$). Flight distances between habitats were greater in 1979 (1741 ± 1354 m) than in 1978 (1156 ± 974 m). In both years, flight distances to riparian roost sites were the longest, followed by those to native grassland. Distances to planted hayland and cornfield were intermediate, and distances to other habitats were shortest.

During the day, cranes fed primarily in native grassland (pasture), hayland, and cornfield (Table 3). Locomotion, which may reflect food searching behavior, was greatest in native grasslands and haylands. Resting occurred primarily in native grasslands and cornfields. Cranes were least often alert in plowed fields (Table 3). Courtship, although rare, was most common in native grasslands and haylands.

Group size and activities.—Frequencies of behaviors during the day varied with flock size (Table 4). Groups of 1–5 and 100–199 individuals fed most, rested least, and were alert most often. Cranes in flocks >200 tended to rest and engage in comfort behaviors such as preening more frequently than those in flocks of other sizes.

DISCUSSION

Spatial relationships.—Sandhill Crane activity ranges in the Platte River Valley were smaller and distances of flights from roosts to feeding grounds were shorter than those reported during fall in North Dakota (Melvin and Temple 1983). These differences may reflect greater abundance of high-energy foods in close proximity to roosts and absence of

TABLE 3

DIURNAL ACTIVITY BUDGETS (% OF TIME) OF STAGING SANDHILL CRANES BY TYPE OF HABITAT ALONG THE PLATTE RIVER, NEBRASKA

Behavior	Habitat[a]					Total	G^b	P
	NG	PHAY	CORN	CULT	PLOW			
Resting	39.4	23.2	36.6	0.7	0.0	19.6	1253	0.001
Feeding	29.9	43.9	20.3	5.6	0.3	42.0	87	0.001
Alert	35.2	41.1	18.3	5.0	0.4	14.4	246	0.001
Calling	34.3	40.0	14.3	11.4	0.0	0.1	4	ns
Courting	26.9	62.7	2.9	7.5	0.0	0.2	32	0.001
Aggression	31.1	42.6	23.0	3.3	0.0	0.2	0	ns
Locomotion	28.7	34.9	28.0	7.5	0.9	11.6	362	0.001
Comfort	47.5	29.2	17.8	4.6	0.9	11.1	503	0.001
Unknown	48.0	24.6	23.5	3.5	0.4	0.8	33	0.001
N	11,934	12,698	8258	1610	136	34,636		
Total %	34.4	36.7	23.8	4.6	0.5			

[a] NG = native grassland; PHAY = planted hayland; CULT = cultivated other than corn; PLOW = plowed land.
[b] $G_{\text{Heterogeneity}} = 1580$, df = 32, $P < 0.001$.

hunting in Nebraska. Waste corn was sufficiently abundant within a radius of a few km of roosts to support energy requirements of thousands of cranes, even where feeding was focused south of the river. Crane densities on the study area ranged up to 12,500 cranes per km of river channel (U.S. Fish and Wildl. Serv. 1981). In the North Platte River Valley, spring staging cranes also acquire dietary needs in close proximity to their roosts (Iverson et al. 1987).

Human disturbance from traffic on I-80 probably was the principal cause of reduced use of habitat north of riverine roosting sites and for the high percentage of peripheral roosts. All nocturnal roosts were within 3 km of I-80. Krapu (pers. obs.) observed that low-flying cranes which flew north from roosts frequently hesitated, turned back, or gained altitude when trying to cross the highway. Birds with central roosts could be expected to travel less and conserve more energy than those with peripheral roosts (Wittenberger and Dollinger 1984), but we found no difference in travel distance between roost types. For cranes, waste corn was highly available during spring, 1978 and 1979, (Reinecke and Krapu 1986), and may have reduced the importance of roost type on foraging efficiency.

Foraging as a factor of crane staging.—We observed that cranes which roosted near each other typically departed in the morning in the same general direction but did not go to the same feeding sites as observed among Common Terns (*Sterna hirundo*) and Ospreys (*Pandion haliaetus*)

TABLE 4

DIURNAL ACTIVITY BUDGETS (% OF TIME) FOR SANDHILL CRANES STAGING ALONG THE PLATTE RIVER, NEBRASKA, BY FLOCK SIZE

Behavior	Flock size					Total	G[a]	*P*
	1–5	6–9	10–99	100–199	200+			
Resting	1.4	27.3	23.7	8.1	19.2	19.6	875.1	0.001
Feeding	54.6	43.4	38.6	55.4	40.0	42.1	241.8	0.001
Alert	16.5	13.2	13.3	17.8	14.5	14.4	45.6	0.001
Calling	0.2	0.0	0.2	0.4	0.1	0.1	28.8	0.001
Courtship	0.3	0.0	0.3	0.5	0.2	0.2	29.5	0.001
Aggression	0.2	0.2	0.1	0.2	0.2	0.2	5.9	ns
Locomotion	22.0	9.2	10.9	11.6	11.8	11.6	111.9	0.001
Comfort	3.5	6.1	12.4	5.4	13.0	11.0	368.0	0.001
Unknown	1.4	0.4	0.3	0.5	1.0	0.8		
N	1250	2877	12,362	3848	14,231	34,568		

[a] $G_{\text{Total}} = 1762$, df = 35, $P < 0.001$; $G_{\text{Heterogeneity}} = 1760$, df = 31, $P < 0.001$.

(Waltz 1987, Hagan and Walters 1990). Rather, flocks of cranes upon reaching the feeding grounds, tended to join existing groups of cranes already on the ground. As a result, large foraging aggregations of cranes became common by mid-morning through local enhancement (Hinde 1961, Wittenberger and Hunt 1985). Use of occupied fields probably increases the foraging efficiency of inexperienced birds because density of waste corn varies much more among fields, depending on post-harvest land use (Baldassarre and Bolen 1984, Reinecke and Krapu 1986) than within a field (Frederick et al. 1984). As a result, cranes that settle into occupied fields are likely to be more successful foragers.

Norling et al. (1991) showed that the variability in duration of departures from nocturnal roosts to foraging sites and percent of cranes leaving roosts after sunrise increased with date and population buildup. Cranes also left roosts later during fog or precipitation. These responses suggest that cranes rely heavily on visual cues to find food. The increased percentage of delayed departures as the number of cranes increased and food availability declined is consistent with our premise of the importance of local enhancement to enhance foraging efficiency. New migrants into the staging area and cranes that have recently switched activity ranges are likely to benefit most by using conspecifics to locate suitable foraging sites.

The availability of macroinvertebrates to cranes is much less predictable and distribution more clumped than that of corn and depend on soil temperature, escape mechanisms of the organisms, and local abundances

(Richter 1958, Edwards and Lofty 1977). Foraging efficiency among cranes seeking macroinvertebrates is more likely to be enhanced by cranes flying or walking to specific sites where concentrated foraging activity is in progress or signs of recent foraging activity are present. Intense probing by Sandhill Cranes in areas with high concentrations of soil invertebrates disturbs the soil surface (G. Krapu, pers. obs.) and may provide visual cues to other cranes seeking animal foods even after the initial foragers have departed. Cranes spent as much time foraging to obtain the 3% of the diet comprised of invertebrates as the 97% formed by corn (Reinecke and Krapu 1986), reflecting the disparate rates of foraging success on invertebrates and corn.

Cranes probably improve their foraging efficiency and reduce energy costs by remaining in the vicinity of their feeding grounds throughout the day. Only 1.7% of the locations of radio-marked cranes between 08:00 and 18:00 h were at communal roosts; most diurnal use of communal roosts occurred during periods when cranes failed to depart at dawn because visibility was poor. Some species are thought to establish centrally located diurnal activity centers (DAC) from which they base their foraging expeditions (Caccamise and Morrison, 1986, 1988; Caccamise 1993). These DACs are proximal to feeding sites and reduce energy spent in flying to different areas. Congregations of cranes in native grasslands and planted haylands near water and feeding grounds during mid-day are suggestive of DACs. Among the activity ranges that we followed, 29 had data that could be inspected for the presence of a DAC. Twelve had sites with concentrated observations on two or more days which are consistent with a DAC, 10 had possible sites but inadequate data, and seven showed no evidence for a DAC. Among European Starlings (*Sturnus vulgaris*), communal roost location is determined primarily by food distribution, and birds are more faithful to their feeding sites than to communal roosts (Morrison and Caccamise 1985), leading Caccamise (1991) to suggest that the information center hypothesis did not adequately explain starling behavior. Crane distribution, however, is determined primarily by availability of suitable communal roosting habitat (Krapu et al. 1984) which is more restricted than is food availability (Krapu et al. 1985). Cranes frequently change communal roosts and foraging sites and both communal roosts and DACs serve as information exchange centers for improving foraging efficiency. The theories of information centers and DACs are not mutually exclusive (Tye 1993), and further research should be conducted to determine the contributions each makes to foraging efficiency in Sandhill Cranes.

Differences in flight distances to specific habitats can indicate the importance of these habitats, presuming that birds will spend greater energy

traveling to more important sites. The higher than expected use of native grasslands and planted haylands relative to their availability reflects the limited distribution of these habitats, together with their importance in supplying macroinvertebrates. Consumption of animal foods high in protein compensates for the low protein content of corn (Reinecke and Krapu 1986). Biomass of macroinvertebrates is relatively low, particularly in wet meadows (Davis 1991), presumably adding to the search time cranes require to satisfy dietary needs.

Influence of predation and behavior on group size.—Models of flocking behavior and predation predict that the proportion of time spent watching for predators should decline with group size and reach an asymptote when the likelihood of spotting a predator no longer increases with group size. We found that cranes spent little time in alert behavior and that the proportion of time spent alert or feeding did not vary consistently with flock size. Similarly, Tacha (1988) did not find a relation between percentage of time in feeding or in alert with flock size and reported that only 0.5% of 1619 alert responses with known causes were in response to predators. The fact that alert did not vary with flock size as predicted also suggests limited vulnerability of cranes to predators that currently exist in the Platte River Valley. Raptors may kill a few cranes (Lewis 1974, Lingle and Krapu 1986), but most data are circumstantial. Only two of 170 Sandhill Cranes (1%) examined by Windingstad (1988) were apparently killed by predators during the nonbreeding season.

At night, cranes roost in riparian sites and semipermanent wetlands (Krapu et al. 1984, Folk and Tacha 1990), where they are protected by a water barrier and open canopy from most predators. Cranes spent less time in alert at night than during the day (8.6% versus 14.4%, G. Krapu, unpubl. data).

Other influences.—Mate finding and behavioral synchronization also have been identified as benefits of communal roosting and flocking (Moynihan 1968). Courtship was rare in our study compared with other behaviors, but it occurs most frequently in spring (Tacha 1988). Pair-bonds in young cranes are typically ephemeral, and several pairings may occur before mates are finally chosen (Nesbitt and Shapiro-Wenner 1987). Staging could facilitate mate selection by attracting numerous birds.

Epizootics have been reported frequently in staging waterfowl (Wobeser 1981). However, disease was not an observed problem in our study, and epizootics have not been reported in Sandhill Cranes. Reported occurrences of botulism, avian tuberculosis, *Salmonella* (Lewis 1974), and of avian cholera (Krapu and Pearson 1981, Kauffeld 1987, Windingstad 1988) are infrequent.

Conservation concerns.—Our findings indicate that staging behavior of

Sandhill Cranes is strongly influenced by the massive anthropogenic alterations that have taken place in the Platte River Valley. To date, habitat loss has caused a major redistribution of cranes (Krapu et al. 1982), but sufficient remaining roosting and foraging habitat continues to attract and support most of the midcontinent population for several weeks each spring. So far, cranes have successfully avoided the energetic consequences and associated displacement that would have resulted from massive habitat loss had an abundant supply of high energy waste corn and adequate sources of protein in native grassland not been available. The status of this important Sandhill Crane staging area remains precarious, however, because of continuing degradation and loss of open river channels and native pastures (Sidle et al. 1989). With continuing habitat loss, crowding will increase and available food supplies may prove inadequate. Human presence in the Platte River Valley has risen dramatically over the past decade due to increased public awareness of cranes (Lingle 1991). The effects of this increased activity on foraging behavior and activity range characteristics have not been measured.

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CONFIRMATION OF ELLIPTICAL MIGRATION IN A POPULATION OF SEMIPALMATED SANDPIPERS

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Abstract.—Using measurements and observations of marked birds we verified the elliptical migration route of some Semipalmated Sandpipers. Bill lengths of spring migrants in Saskatchewan averaged longer than those of fall migrants, suggesting a mix of short-billed western and longer-billed central Arctic breeders in the spring, and a greater proportion of western breeders in the fall. A number of birds captured during spring migration in Saskatchewan (presumably central Arctic breeders) were found staging in eastern Canada in the fall. In contrast, no birds captured during fall migration in Saskatchewan were seen north of Maryland on the east coast in the fall. Other Saskatchewan spring migrants (presumably western breeders) returned south through the prairies. These findings emphasize the interrelatedness of major migratory staging areas during spring and fall migration for this species.
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Semipalmated Sandpipers (*Calidris pusilla*) breed across northern Canada and Alaska and winter primarily in northeastern South America (Phillips 1975, AOU 1983, Morrison 1984, Godfrey 1986, Morrison and Ross 1989). Although they are one of the most common shorebirds seen during migration in North America, much remains unknown about the migratory routes and wintering areas of different breeding populations. Measurements of live birds and museum specimens, as well as resightings of birds marked and banded in eastern Canada and the eastern seaboard of the United States, suggest the following migration routes. In the fall, most central and all eastern breeders return south via the Atlantic coast, staging primarily at the Bay of Fundy, Canada. Western breeders apparently migrate south through the interior of North America. In the spring, eastern breeders follow an Atlantic route from northern South America to the eastern United States at Delaware Bay, New Jersey, south of the Bay of Fundy. Central and western arctic breeders appear to migrate north through the interior of North America. Therefore the migration routes of central and eastern breeders follow somewhat of an elliptical pattern, being farther east in the fall than in spring (Harrington and Morrison 1979, Lank 1983, Morrison 1984, Hicklin 1987).

Few banding studies have been carried out in the interior of North America, with the exception of Cheyenne Bottoms, Kansas (Martinez 1979), and Sibley Lake, North Dakota (Lank 1983). Very few resightings of birds banded in these areas have been published, although these records

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have supported the suggested migration routes of fall migrants (Lank 1983, and in Morrison 1984). Almost no information is available on spring migrants in the prairies. Therefore, the purpose of this study is to report measurements and resightings of Semipalmated Sandpipers marked in Saskatchewan during both spring and fall migration, and to determine whether these results support the suggested migration routes for different breeding populations of this species.

STUDY AREA AND METHODS

The Quill Lakes in Saskatchewan (54°N, 104°W) consist of a complex of three alkaline lakes with associated marshy wetlands, about 200 km east of Saskatoon. Big Quill Lake is approximately 27 km by 18 km, Middle Quill 6 km by 3 km, and Little Quill 24 km by 3 km. Salinity levels are variable, differing among lakes and water levels (Morrison et al. 1991). Numbers of Semipalmated Sandpipers migrating through the Quill Lakes in the spring and fall appear to vary among years, but range from tens of thousands in the spring to less than five thousand in the fall (unpubl. data).

Shorebirds were captured at Little Quill Lake (LQL) from 1988 to 1992. Since sample sizes are greatest from 1990 to 1992, and measurements were standardized in those years, we present data only from 1990, 1991, and 1992. Spring migrants were caught in 1990 (26 May–1 June) and in 1992 (16 May–3 June). Fall migrants were sampled in 1990 (16 July–23 August) and 1991 (11 July–26 August). All birds were captured with mistnets, primarily at night.

Birds were given a metal band (usually stainless steel), one or two white plastic (darvic) leg flags, and one color band (red or green). Measurements taken included wing length (±1 mm, maximum chord: flattened and straightened) and bill length (±0.1 mm, exposed culmen: feathering to tip). Birds were aged by plumage characteristics (Prater et al. 1977), dyed with a pattern of picric acid (yellow-orange) on their underparts, and released 0.5 to 6 h later (usually <2 h). Sex was determined by internal examination in a small set of birds collected for another study.

CLGT measured virtually all birds in 1990 and 1992, and HLD, GB (G. Beyersbergen) and CLGT all birds in 1991. Several series of birds were measured by these three researchers in 1991 to assess differences in measuring, and all wing lengths were standardized to those of CLGT. The few wing measurements taken by others were not used. Coefficients of variation (CV) were calculated for each season-year-age group (e.g., fall 1990 adults) and compared to each other using the methods described by Dow (1976).

RESULTS

Numbers marked.—During spring migration, 400 adult Semipalmated Sandpipers were marked in 1990 and 324 in 1992. During fall migration, most Semipalmated Sandpipers captured were juveniles: 30 adults and 1309 juveniles in 1990, 57 adults and 491 juveniles in 1991.

Spring migrants at Little Quill Lake.—Sightings of birds marked at LQL during spring migration are shown in Fig. 1 and listed in Table 1. Six birds at LQL during spring migration were observed or banded in South America: five in French Guyana and one in Peru. The remaining reports of birds marked at LQL in spring were seen during fall migration:

three in Ontario and New York, five in the Bay of Fundy and northeast coast of the United States, and four in the interior of North America.

Fall migrants at Little Quill Lake.—A number of birds banded during fall at LQL (Table 2, Fig. 2) were seen during late fall and winter near and in wintering areas. Four birds banded as adults were observed in French Guyana, and one banded at LQL as a juvenile was found dead in French Guyana two years later. The adult observed on 8 October 1992 was seen in the same flock as a bird marked at LQL in the spring of 1990 (A. LeDreff). Four more birds were recovered in Guyana: three banded as juveniles and one as an adult. Another bird was seen in Aruba, juveniles in Cuba and Puerto Rico, and an adult was from Venezuela.

Twelve Semipalmated Sandpipers banded at LQL in the fall of 1988 were observed at Iona Island, British Columbia, from 27 June to 1 July 1989 (R. Toochin). A bird banded as a juvenile was seen at age two with a brood at Prudhoe Bay, Alaska.

During fall migration, two birds (one adult and one yearling banded as a juvenile at LQL) were observed in Tennessee. Seven more birds (four juveniles, three of unknown age) were sighted along the east coast of the United States (Maryland, Virginia, North and South Carolina) later in the same fall that they were banded at LQL.

Measurements.—Years were not combined due to significant differences in seasons between years (ANOVA, $P < 0.05$). An analysis of variance for unbalanced data (SAS Institute 1988) demonstrated that year ($P < 0.0001$), season ($P < 0.03$), and age ($P < 0.02$) were all significant effects on wing length, although year appeared most important. However, for bill length, only season was a significant effect ($P < 0.0001$), not year ($P < 0.19$) or age ($P < 0.95$). Therefore, spring and fall birds differed in size, particularly with respect to bill length, with spring migrants averaging larger than those captured in fall (Table 3). Differences between years may be due to varying proportions of each sex.

Coefficients of variation for each season-year-age were compared to each other with respect to wing and bill length (Table 3). Only one comparison of 30 was significant (bill length: 1992 spring adults vs 1990 fall juveniles, $t = 2.5$, $P < 0.02$, two-tailed test). Therefore there were virtually no significant differences between seasons in coefficients of variation.

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FIG. 1. Observations of Semipalmated Sandpipers banded at Little Quill Lake, Saskatchewan, during spring migration. The banding site (May/June) is marked by a star. Birds observed during the fall or winter (July to March) are indicated by full triangles with point downwards, and those seen during spring or summer (April to June) by empty triangles pointing upwards.

TABLE 1

RESIGHTINGS OF SPRING MIGRANTS FROM LITTLE QUILL LAKE (LQL), SASKATCHEWAN

Banding age/location/date	Observation location/date	Observer or bander
	Winter	
Adult/LQL/May–June 1990	Kourou, French Guyana/1 Oct. 1990	A. LeDreff
Adult/LQL/May–June 1990	Kourou, French Guyana/22–25 Apr. 1991	A. LeDreff
Adult/LQL/May–June 1990	Kourou, French Guyana/19 Sept.–28 Oct. 1991	A. LeDreff
Adult/LQL/May–June 1992	Kourou, French Guyana/8 Oct. 1992	A. LeDreff
Adult/Kourou, French Guyana/26 Oct. 1992	LQL/26 May 1992	A. LeDreff
?/Peru/?	LQL/24 May 1992	G. Beyersbergen
	Fall (eastern)	
Adult/LQL/May–June 1990	Montezuma Wildl. Refuge, New York/25 Aug. 1990	G. Wolfred & G. Butcher
Adult/LQL/May–June 1992	Cranberry Marsh, Whitby, Ontario/6–7 Aug. 1992	M. Bain & P. Holder
Adult/LQL/May–June 1992	Ottawa Beach, Ottawa, Ontario/4 Aug. 1992	T. Beck
Adult/LQL/May–June 1990	Grand Manan Is., New Brunswick/6–10 Aug. 1990	L. White
Adult/LQL/May–June 1990	Grand Manan Is., New Brunswick/7 Aug. 1990	L. White
Adult/LQL/May–June 1990	Evangeline Beach, Nova Scotia/14 Aug. 1990	J. Tufts
?/Dorchester Cape, New Brunswick/Fall 1989	LQL/31 May 1990	P. Hicklin
Adult/Stratford Pt., Connecticut/6 Aug. 1984	LQL/27 May 1990	C. Trichka
	Fall (central)	
Adult/LQL/May–June 1990	LQL/23 July 1990	P. Chittick
Adult/LQL/May–June 1990	Fargo Sewage Lagoons, North Dakota/22 July 1990	M. Bergen
Adult/LQL/May–June 1992	LQL/24 July 1992	T. Horsley
Adult/LQL/July–Aug. 1988	LQL/17 May 1990	H. L. Dickson

We also compared measurements of Semipalmated Sandpipers of known sex from LQL (Table 4). Analysis of variance indicated a significant effect of sex on wing length ($P < 0.03$) but no significant effect of season ($P = 0.14$). Analysis of variance on bill length indicated a highly significant effect of sex ($P < 0.0001$) and also a smaller, but significant, effect of season on bill length ($P < 0.01$).

DISCUSSION

Observations of Semipalmated Sandpipers marked at LQL support the elliptical migration pattern of central breeders suggested by Harrington and Morrison (1979). Fall migrants from the Quill Lakes area flew south through Tennessee, Maryland, North Carolina, South Carolina, and Virginia, and overwintered in northern South America. The only birds observed in Tennessee were seen as adults, even though many more juveniles than adults were marked during fall migration at LQL, and only juveniles were definitely identified as to age on the southeastern seaboard of the United States. Perhaps adults migrating from Saskatchewan in the fall fly south farther inland then juveniles, which appear to migrate down the coast.

Semipalmated Sandpipers migrating north through the Quill Lakes in spring, flew south either through the interior of North America (Saskatchewan, North Dakota) or farther east (New York, Ontario, New Brunswick, Nova Scotia, Connecticut). Many sightings were considerably farther north and east on the eastern seaboard of the United States and Canada than were those of spring-marked LQL birds. At least some fall LQL birds also wintered in northern South America.

Most Semipalmated Sandpipers winter in northern South America along the coasts of Suriname, Guyana, and French Guyana (Morrison and Ross 1989). Western breeders are thought to winter farther west than eastern and central Arctic birds (Lank 1983, Morrison 1984, see also Resende et al. 1989). We have no evidence that fall migrants at LQL generally winter farther west than spring migrants. However, discovery of marked birds on the wintering grounds is dependant on uneven reporting of band recoveries (primarily Guyana) and distribution of observers (primarily French Guyana at present). More fall-marked LQL birds may winter in northwestern South America but go unreported. Nevertheless, if LQL fall migrants are western breeders, then some western breeders do winter in French Guyana. In fact, a bird banded during spring migration at LQL, and one banded there in the fall, were observed in a single flock in French Guyana (A. LeDreff, pers. comm.).

It is curious, considering that twenty times more juveniles than adults were marked during fall migration at LQL, that four of five LQL birds

TABLE 2
RESIGHTINGS OF FALL MIGRANTS FROM LITTLE QUILL LAKE (LQL), SASKATCHEWAN

Banding age/location/date	Observation location/date	Observer or bander
	Winter	
Adult/LQL/July–Aug. 1990	Kourou, French Guyana/4–19 Sept. 1990	A. LeDreff
Adult/LQL/July–Aug. 1990	Kourou, French Guyana/21 Nov. 1990	A. LeDreff
Adult/LQL/July–Aug. 1990	Kourou, French Guyana/8 Oct. 1992*	A. LeDreff
Adult/LQL/July–Aug. 1991	Kourou, French Guyana/23 Sept.–18 Nov. 1991	A. LeDreff
Adult/LQL/3 Aug. 1989	Georgetown, Guyana/22 Sept. 1991	R. Baksh
Adult/Venezuela/?	LQL/5 Aug. 1988	H. L. Dickson
?/LQL/July–Aug. 1988	Aruba/17–19 Sept. 1988	A. Spaans
Juvenile/LQL/10 Aug. 1990	Guyana/12 June 1992	J. Chinamootoo and C. Berbice
Juvenile/LQL/7 Aug. 1990	Georgetown, Guyana/9 Sept. 1990	T. Singh
Juvenile/LQL/5 Aug. 1988	Nigg, New Shine, Guyana/17 Oct. 1989	S. Sasmareni and C. Berbice
Juvenile/LQL/18 Aug. 1990	Kourou, French Guyana/28 Sept. 1992	A. LeDreff
Juvenile/LQL/19 Aug. 1990	S. Miguel Parada, Cuba/13 Sept. 1990	L. D. Melian
Juvenile/LQL/July–Aug. 1991	Boqueron, Puerto Rico/2–12 Oct. 1991	B. Harrington
Juvenile/LQL/18 Aug. 1991	Wilhelmina Str., Suriname/24 Oct. 1992	R. Mohabir
	Spring/Summer	
12 birds/LQL/July–Aug. 1988	Iona Is., British Columbia/27 June–1 July 1989	R. Toochin
Juvenile/LQL/July–Aug. 1990	Prudhoe Bay, Alaska (with brood)/4 July 1992	D. Troy
	Fall	
Adult/LQL/July–Aug. 1990	Ensley Sewer Lagoons, Memphis, Tennessee/15–17 Aug. 1992	J. Wilson
?/LQL/July–Aug. 1990	Easton Sewage Lagoon, Maryland/15 Sept. 1990	M. O'Brien
?/LQL/July–Aug. 1989	Silver Bluff Plantation, Jackson, South Carolina/2 Aug. 1989	D. Young
?/LQL/July–Aug. 1990	S. Nags Head Ocean Beach, North Carolina/23 Sept. 1990	R. DeVeau
Juvenile/LQL/July–Aug. 1991	Ensley Sewer Lagoons, Memphis, Tennessee/26 July 1992	J. Wilson
Juvenile/LQL/July–Aug. 1990	Easton Sewage Lagoon, Maryland/11–15 Sept. 1990	M. O'Brien
Juvenile/LQL/July–Aug. 1990	Cape Hatteras Is., South Carolina/24 Sept. 1990	L. Stenzel and G. Page
Juvenile/LQL/July–Aug. 1990	Chincoteague Natl. Wildl. Refuge, Virginia/27 Sept. 1990	L. Stenzel and G. Page
Juvenile/LQL/July–Aug. 1991	Pea Is. Natl. Wildl. Refuge, North Carolina/20 Sept. 1991	S. Dinsmore

* Seen in same flock as bird marked at LQL in Spring 1990 (A. LeDreff).

observed in French Guyana were banded as adults. Possibly juveniles and fall adults at LQL are from separate breeding populations, although measurements were not consistently different (Table 3). Perhaps wintering areas differ between adults and juveniles, as migration routes sometimes do (above, and Morrison 1984), since the one bird banded as a juvenile was not recovered in French Guyana until several years later. Semipalmated Sandpipers from western breeding areas may not migrate as far east as adults in northern South America.

Twelve birds banded at LQL during the fall of 1988 were observed near Vancouver, British Columbia, in late June the following year. This is very late for spring migration, since virtually all Semipalmated Sandpipers should have initiated nests by this time (Gratto-Trevor 1992). It is very early for southward migration, even of failed breeders. It is possible that these birds were yearlings, as almost 90% (825/957) of Semipalmated Sandpipers banded at LQL in 1988 were juveniles. This, then, may represent a late or partial northwards migration of nonbreeders. Although some Semipalmated Sandpipers breed as yearlings, most do not migrate or attempt to breed until age two or older (Gratto and Morrison 1981, Gratto 1988). Only small numbers of Semipalmated Sandpipers are known to migrate regularly through the southern coast of British Columbia during both spring and fall migration, and there is some suggestion that migration "strength" varies from year to year (Campbell et al. 1990). Thus, although some birds banded in Saskatchewan during fall migration have been observed in southern British Columbia, it is doubtful that this represents the normal migration route of most western breeders.

Data are few, but numbers of shorebirds migrating through the Quill Lakes area in spring do not appear to be consistent from year to year, even when habitat conditions seem favorable (Gratto-Trevor and Dickson, unpubl. data). We thought that in years of unfavorable water conditions at Cheyenne Bottoms, Kansas (a major interior spring staging site), larger numbers of shorebirds would stage at the Quill Lakes. This does not appear to be the case. Water conditions at Cheyenne Bottoms in spring 1988 were optimal, and upwards of 250,000 shorebirds were present (D. Helmers, pers. comm.). Over 150,000 birds were also seen that spring at Big Quill Lake (Morrison et al. 1991). In 1992, wetlands at Cheyenne Bottoms were dry until late May, and virtually no shorebirds were seen there that year (H. Hands, pers. comm.). Numbers at Big Quill Lake were also very low, even though suitable habitat was available (G. Beyersbergen, pers. comm.). It is possible that in some years, particularly when spring water levels in the interior of North America are unsuitable for foraging, Semipalmated Sandpipers are more likely to migrate along a broad front, spreading out over the prairies and into southern British

TABLE 3

MEASUREMENTS OF SEMIPALMATED SANDPIPERS CAPTURED AT LITTLE QUILL LAKE, SASKATCHEWAN, FROM 1990 TO 1992

Season	Year	Age	N	Mean	SD	Range	CV
			Wing (mm)				
Fall	1990	Adult	30	99.3	2.3	95–105	2.3
	1991	Adult	57	97.3	2.5	92–103	2.6
	1990	Juvenile	1309	98.2	2.3	91–106	2.3
	1991	Juvenile	491	99.0	2.3	92–105	2.3
Spring	1990	Adult	400	98.5	2.4	92–105	2.4
	1992	Adult	325	99.0	2.3	92–105	2.3
			Bill (mm)				
Fall	1990	Adult	33	18.8	1.3	16.5–21.1	7.0
	1991	Adult	55	18.4	1.4	16.2–21.8	7.6
	1990	Juvenile	1175	18.5	1.2	15.0–22.5	6.5
	1991	Juvenile	485	18.7	1.2	15.7–22.0	6.4
Spring	1990	Adult	400	19.1	1.2	15.9–22.9	6.3
	1992	Adult	325	18.9	1.1	15.9–22.2	5.8

Columbia. For example, in the spring of 1989, the year fall migrants from LQL were seen in British Columbia, conditions for migrants at Cheyenne Bottoms were very poor (D. Helmers, pers. comm.).

Semipalmated Sandpipers have a cline in wing and bill length across their breeding range, with birds from the east averaging larger than those from the west. However, since wings and bills of females are on average larger than those of males in each population, measurements of western males and eastern females overlap greatly (Harrington and Morrison 1979, Godfrey 1986). In general, there was a greater average bill length of spring versus fall migrants at LQL (Table 3). The difference between spring and fall migrants was more pronounced using known-sex birds (Table 4), and indicates that at LQL spring flocks contain breeders from farther east than do fall flocks. This agrees with both the proposed elliptical migration and the sightings of LQL birds. Semipalmated Sandpipers migrating through LQL in the fall are most likely from western breeding areas. Spring mi-

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FIG. 2. Observations of Semipalmated Sandpipers banded at Little Quill Lake, Saskatchewan, during fall migration. The banding site (July/August) is marked by a star. Birds observed during the fall or winter (July to March) are indicated by full triangles with point downwards, and those seen during spring or summer (April to June) by empty triangles pointing upwards.

TABLE 4

MEASUREMENTS OF MALE AND FEMALE SEMIPALMATED SANDPIPERS COLLECTED AT LITTLE QUILL LAKE, SASKATCHEWAN FROM 1990 TO 1992

Season	Sex	N	Wing (mm)			Bill (mm)		
			Mean	SD	Range	Mean	SD	Range
Fall	Female	12	97.8	2.2	93–102	18.9	1.0	18.1–21.2
	Male	8	96.5	1.8	95–100	17.6	0.6	16.7–18.5
Spring	Female	5	100.0	2.3	97–102	20.0	0.6	19.0–20.6
	Male	8	96.9	2.4	95–101	18.1	0.9	16.7–19.1

grants appear to consist of a higher proportion of the larger central breeders, with some western birds also included (see Morrison 1984: Fig. 8). There was no seasonal difference in coefficients of variation, suggesting as much mixing of populations in spring as in fall, inconsistent proportions of each sex, or a greater variation in "western" breeders. With the information presently available, we cannot differentiate among these possibilities.

Hundreds of thousands of Semipalmated Sandpipers stage in the Bay of Fundy during fall migration, but almost none are present in the spring (Hicklin 1987). Ice gouging of mudflats and the lateness of spring in eastern Canada typically result in a paucity of food for shorebirds in the intertidal zone at that time of the year (Peer et al. 1986, Wilson 1989, P. W. Hicklin, pers. comm.). However, high invertebrate concentrations (primarily a burrowing amphipod, *Corophium volutator* L.) in the extensive mudflats of the Bay of Fundy in late summer (Peer et al. 1986, Mathews et al. 1992) attract large numbers of birds in the fall. This variation in food availability is thought to be a major factor influencing migration routes and elliptical migration in at least some populations of Semipalmated Sandpipers (Morrison 1984).

In conclusion, sightings of birds banded at Little Quill Lake, Saskatchewan, have confirmed the elliptical migration pattern of central Arctic breeding Semipalmated Sandpipers proposed in 1979 (Harrington and Morrison 1979). However, a number of individuals, probably western breeders, retrace their northward migration in the fall. Several birds banded in Saskatchewan in the fall were observed in southern British Columbia the following year. Nevertheless, due to the generally low numbers of Semipalmated Sandpipers seen on the west coast in the spring, and the timing of the Little Quill Lake sightings (very late spring or very early fall), it is unlikely to indicate a consistent pattern of elliptical migration by western breeders. Variation in "strength" of Semipalmated Sandpiper

migration on the west coast of Canada may result from variability in habitat suitability (due to drought) in the interior of North America. These results emphasize the inter-relatedness of staging sites in the western hemisphere for populations of Semipalmated Sandpipers. Negative impacts at a single important site could greatly affect a number of different populations of the species that use the area at different times of the year.

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MIGRATING SHOREBIRDS AND HABITAT DYNAMICS AT A PRAIRIE WETLAND COMPLEX

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ABSTRACT.—We examined the responses of migrating shorebirds to habitat dynamics in a wetland complex on the Great Plains during 1989–1992. Availability of habitat was variable within and between seasons, but fluctuations in habitat were dampened when wetlands were considered as a complex rather than individually. Shorebirds exhibited an ability to colonize available habitat opportunistically, to occupy wet mud/shallow water habitats that became available during their residency period regardless of wetland history, and to use wet mud/shallow water habitat almost immediately upon its appearance. We found a significant relation between number of shorebirds and the area of wet med/shallow water habitat, regardless of dramatic changes in habitat. Management for continental stopover sites for shorebirds requires the maintenance of complexes of potential habitat to assure resource alternatives for birds as local conditions vacillate. *Received 11 Jan. 1993, accepted 20 July 1993.*

During migration, several species of Arctic-breeding shorebirds use freshwater wetlands in the North American interior as staging or stopover sites for replenishing fat reserves. Without food resources to "refuel", these birds would be unable to complete their journeys to breeding or wintering grounds. The protection of stopover resources for migrating shorebirds is critical to the survival of many of these species (Myers 1983). The first step in this protection effort, the identification of sites that traditionally support large populations during migration and the protection of these sites as a network (Myers et al. 1987), is being undertaken specifically by the Western Hemisphere Shorebird Reserve Network and, in general, by other wetland conservation programs (Bildstein et al. 1991).

Shorebirds migrating across continental wetland habitats encounter temporally and spatially dynamic wetlands (Fredrickson and Reid 1990, Szaro 1990, Skagen and Knopf 1993). The dynamic and unpredictable nature of interior wetlands and the rapid rate of loss and alteration of wetlands in these regions (Tiner 1984, Dahl 1990) combine to make the above "reserve" management approach problematic. Species that use disjunct patches of changing habitat in an irregular fashion, as seen especially during migration, may be the most difficult to protect (Takekawa and Beissinger 1989).

In this paper, we evaluate the predictability of stopover sites in the Great Plains and responses of migrating shorebirds to habitat dynamics. We hypothesized that when resource availability changes rapidly, tran-

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sitory populations respond to wetland dynamics opportunistically rather than exhibit strong annual site fidelity. More specifically, if migrating shorebirds use habitats opportunistically, we expect them to use available habitat regardless of the recent wetland history. Thus, although some wetlands provide no wet mud/shallow water habitat for shorebird foraging during all or parts of sequential migration periods, we expect shorebirds to find and use these wetlands when wet mud/shallow water habitat again becomes available during migration. Second, we hypothesized that if habitats are constantly fluctuating and birds are opportunistic, a positive correlation between birds and wet mud/shallow water habitat would occur. Alternatively, shorebirds that use sites traditionally would be tied to habitats that may be marginal in some years, and no relationship between numbers of birds and area of wet mud/shallow water habitat would be apparent.

STUDY AREA AND METHODS

Quivira National Wildlife Refuge, Stafford County, Kansas (38°10′N, 98°40′W), is a 8830-ha refuge of the U.S. Fish and Wildlife Service (Fig. 1). Forests and croplands are interspersed with 30 water units ranging in size from 1 to 600 ha and Rattlesnake Creek that flows intermittently. Vegetation in and surrounding the wetlands includes wetland plant species in the genera *Distichlis, Spartina, Typha, Carex*, and *Juncus*.

Shorebirds occurring in water units and in extensive mudflats and marshes throughout the refuge were surveyed from a vehicle and on foot 1–2 times weekly during late summer-fall migration (August through mid-October) 1989–1991 and spring migration (April to early June) in 1990–1992. Because the survey areas are relatively open and unvegetated, we were able to make complete counts of shorebirds (see also Colwell and Oring 1988, Hands et al. 1991). When feasible, we identified all individuals. When large numbers occurred or when birds were too distant to identify individually, we estimated total numbers of birds categorized by relative body size. We extrapolated to the larger group based on subsamples of birds.

We estimated dimensions of wetland units from maps and by pacing. During surveys, we estimated the percentage of each unit that comprised the following habitat types: dry mud, wet mud, mud-water film (1–2 cm of water interspersed with mud), shallow water (2–8 cm), and deep water (>8 cm) and noted presence of vegetation. We collected information on habitat availability at Quivira NWR on ten small (<5 ha) water units that were present all six seasons and on eight additional ephemeral wetlands during one or more seasons (Fig. 1). We quantified habitat availability only in the small discrete water units, not in the more extensive mudflats and marshes on the refuge (Fig. 1).

We operationally define the terms "suitable habitat" and "suitable wetland" to refer to wet mud-shallow water habitats with little or no vegetation, habitats that are generally

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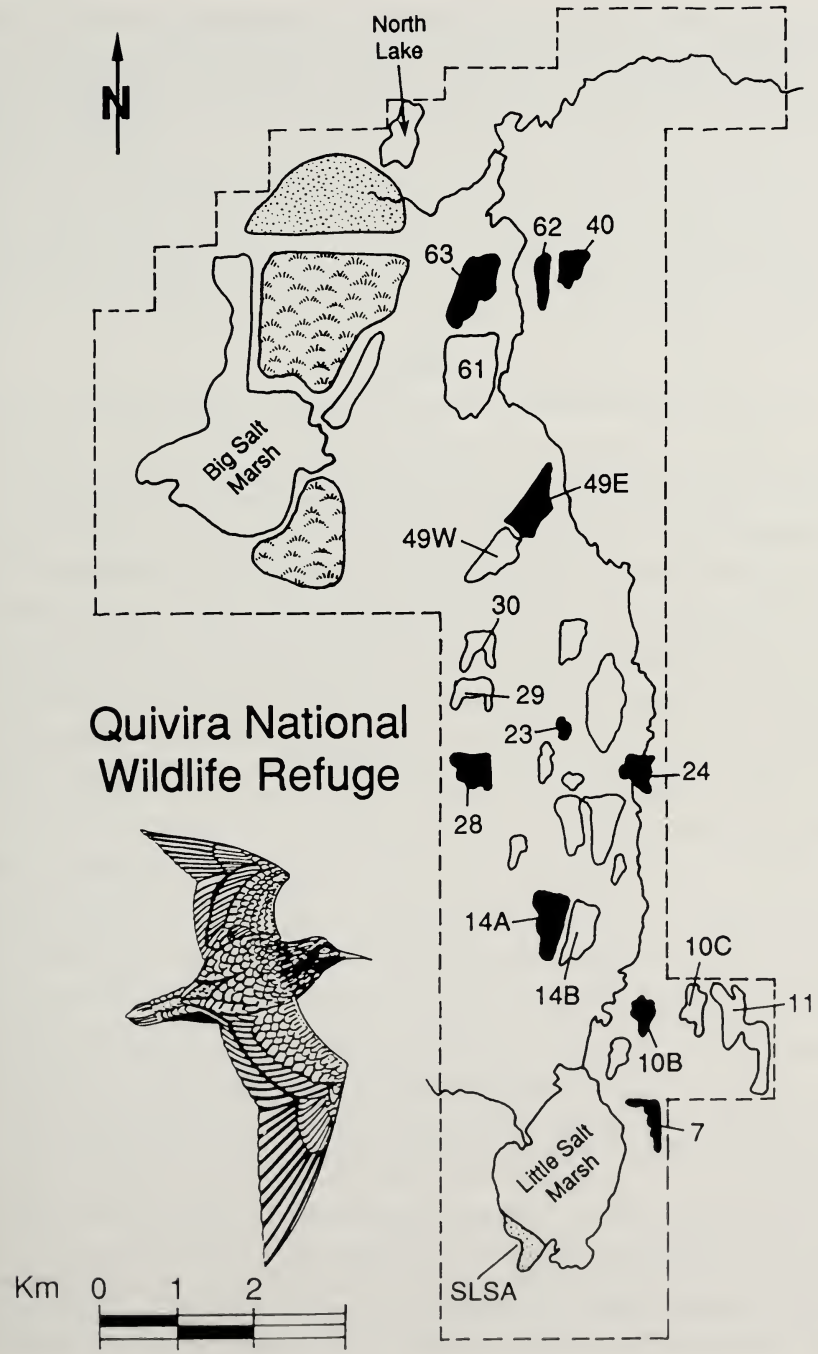
FIG. 1. Map of study site at Quivira National Wildlife Refuge, central Kansas. Eighteen individual water units are identified by number, and the ten units with extensive coverage are darkened.


North Lake
N
62
40
63
61
Big Salt Marsh
49E
49W
30
29
23
24
28
Quivira National Wildlife Refuge
14A
10C
14B
11
10B
7
Little Salt Marsh
SLSA
Km 0 1 2

attractive to most shorebird species (Colwell and Oring 1988). Below we use these terms interchangeably with "shorebird habitat" and "wet mud/shallow water."

We documented the sequential pattern of habitat availability in wetlands during six migration seasons, and noted shorebird use of wetlands that had no wet mud/shallow water habitat earlier in a season or in previous seasons. We also examined bird responses to the relative distribution of habitats in seasons when wet mud/shallow water habitat was available in water units. First, we selected five surveys in each season that corresponded with large increases in numbers of birds, suggesting the presence of new arrivals, and large overall counts on the refuge. Because many birds had recently arrived and because time intervals between these selected surveys averaged 12 days, we considered the surveys independent of each other. We formed three categories of shorebirds based on their primary patterns of habitat use (Table 1). All statistical analyses were performed using SYSTAT 5.0.

RESULTS

Quivira National Wildlife Refuge provided important stopover habitat for a total of 35 species during spring and late-summer/fall migrations (Table 1). During spring 1990, the season of heaviest shorebird use, peak counts totalled 15,633 birds. Peak numbers of individual species were generally higher in spring than in fall, and species composition varied between seasons. In both spring and fall, Long-billed Dowitchers (*Limnodromus scolopaceus*), Stilt Sandpipers (*Calidris himantopus*), Semipalmated Sandpipers (*C. pusilla*), and Wilson's Phalaropes (*Phalaropus tricolor*) were among the most common birds. White-rumped Sandpipers (*C. fuscicollis*) and Baird's Sandpipers (*C. bairdii*) were common only in spring, while Western Sandpipers (*C. mauri*) and Least Sandpipers (*C. minutilla*) were common only in fall. Shorebirds commonly associated with wet mud/shallow water habitat comprised more than 80% of peak numbers of birds (Table 1).

Habitat variability within and between seasons.—The condition of the wetlands varied considerably between the six migration seasons. During spring 1990, all units were full of water and had no wet mud/shallow water habitat suitable for shorebird foraging. In late summer–fall 1991, most small units were dry. Collectively, in a total of 74 unit-seasons (one water unit for one migration season), 36 had no wet mud-shallow water habitat. In 16 unit-seasons, wet mud/shallow water habitat was present initially but eventually disappeared, and in 18 unit-seasons, wet mud/shallow water habitat was absent initially but appeared later in the season. Only four unit-seasons had available habitat throughout a migration season.

The amount of wet mud/shallow water habitat in the water units often fluctuated during the 2–3 month migration season, as illustrated by 11 wetlands in fall 1990 (Fig 2). Because the amount of wet mud/shallow water habitat in individual wetlands was dependent on wetland topography and water levels, the presence of habitat across the various wetlands

was not always synchronized (Fig. 2). At times, deeper wetlands had wet mud/shallow water habitat only during drying cycles when shallower wetlands completely dried. The patterns of water level fluctuations in individual wetlands were dramatically different between the six migration seasons (Fig 3).

However, fluctuations in the amount of wet mud/shallow water habitat were dampened at a larger geographical scale (Fig 4). As a result, there was high likelihood that wet mud/shallow water habitat was available in at least one wetland in the complex at a given point in time. Wet mud/shallow water habitat was generally available within the complex of 10 wetlands throughout four of the six migration seasons in this study (Fig. 5). When also considering the extensive mudflats and marshes on the refuge, suitable habitat occurred somewhere on the refuge in all six seasons.

Bird distribution relative to wetland history.—In general, shorebirds responded quickly to the first appearance of wet mud/shallow water habitat in a wetland in a given season (Table 2). In 15 of the 18 unit-seasons in which suitable habitat was absent initially but later appeared during that season, some shorebirds responded immediately (were present in the first survey after the appearance of wet mud/shallow water habitat). In only two cases, one survey elapsed before any shorebirds appeared, and in one case, shorebirds did not use the wetland at all, possibly because the habitat appeared late in the season when few birds remained in the area. Some species responded more consistently than others. Baird's Sandpipers, White-rumped Sandpipers, Lesser Yellowlegs (*Tringa flavipes*), and Long-billed Dowitchers appeared immediately in more than half the new suitable habitats in all seasons (Table 2), whereas Semipalmated Sandpipers and Least Sandpipers did not.

On average, only four days elapsed between the two surveys bracketing the appearance of habitat and birds. There was a broad range in numbers of individual birds that responded within the first few days of habitat availability (median = 28, range 3–1122). The species that occurred in the largest assemblages were Long-billed Dowitchers, Lesser Yellowlegs, Semipalmated Sandpipers, and Baird's Sandpipers.

Shorebirds also responded quickly to the first appearance of wet mud/shallow water habitat in a given wetland in several seasons (Table 2). During spring of 1992, three suitable wetlands had no wet mud/shallow water habitat during the preceding spring migration season, and four other suitable wetlands had no wet mud/shallow water habitat during two preceding spring seasons. In fall 1990, nine suitable wetlands had no wet mud/shallow water habitat during one preceding fall migration period. Even though no shorebirds had used these wetlands during spring (or fall)

TABLE 1

SHOREBIRDS AT QUIVIRA NATIONAL WILDLIFE REFUGE, KANSAS, DURING SIX MIGRATION SEASONS, 1989–1992, CATEGORIZED ACCORDING TO ASSOCIATION WITH THREE HABITAT TYPES

		Peak counts					
		Fall			Spring		
Alpha code	Common name (scientific name)	1989	1990	1991	1990	1991	1992
	Uplands, pond margins, dry mud						
SNPL	Snowy Plover (*Charadrius alexandrinus*)	83	85	74	118	104	112
PIPL	Piping Plover (*C. melodus*)	2	0	0	2	0	1
KILL	Killdeer (*C. vociferus*)	165	131	160	38	50	66
SPSA	Spotted Sandpiper (*Actitis macularia*)	15	8	18	23	20	31
UPSA	Upland Sandpiper (*Bartramia longicauda*)	3	2	0	2	1	1
BBSA	Buff-breasted Sandpiper (*Tryngites subruficollis*)	0	0	1	0	0	0
COSN	Common Snipe (*Gallinago gallinago*)	15	6	0	1	1	2
AMWO	American Woodcock (*Scolopax minor*)	0	0	0	2	0	0
	Wet mud–shallow water						
SEPL	Semipalmated Plover (*Charadrius semipalmatus*)	12	16	16	47	17	34
SESA	Semipalmated Sandpiper (*Calidris pusilla*)	664	600	561	1979	2470	3351
WESA	Western Sandpiper (*C. mauri*)	780	876	208	218	0	12
LESA	Least Sandpiper (*C. minutilla*)	1010	524	788	262	238	0
WRSA	White-rumped Sandpiper (*C. fuscicollis*)	0	0	0	5082	4867	1771
BASA	Baird's Sandpiper (*C. bairdii*)	258	229	189	1366	716	1284
BBPL	Black-bellied Plover (*Pluvialis squatarola*)	11	300	0	195	14	20
LEGP	Lesser Golden Plover (*P. dominica*)	7	0	1	10	0	2
GRYE	Greater Yellowlegs (*Tringa melanoleuca*)	122	122	100	155	221	184
LEYE	Lesser Yellowlegs (*T. flavipes*)	300	454	213	818	509	391
SOSA	Solitary Sandpiper (*T. solitaria*)	11	9	1	2	0	5
RUTU	Ruddy Turnstone (*Arenaria interpres*)	0	1	0	9	0	0

TABLE 1
CONTINUED

Alpha code	Common name (scientific name)	Peak counts					
		Fall			Spring		
		1989	1990	1991	1990	1991	1992
REKN	Red Knot (*Calidris canutus*)	9	0	0	0	0	0
SAND	Sanderling (*C. alba*)	17	39	5	22	0	0
PESA	Pectoral Sandpiper (*C. melanotos*)	68	37	49	105	44	20
DUNL	Dunlin (*C. alpina*)	0	0	1	25	5	0
STSA	Stilt Sandpiper (*C. himantopus*)	1152	713	68	1088	813	1175
SBDO	Short-billed Dowitcher (*Limnodromus griseus*)	0	0	0	5	0	0
LBDO	Long-billed Dowitcher (*L. scolopaceus*)	1165	1113	1975	1875	511	637
	Deeper and open water						
BNST	Black-necked Stilt (*Himantopus mexicanus*)	34	35	87	2	31	23
AMAV	American Avocet (*Recurvirostra americana*)	99	260	558	217	86	141
WILL	Willet (*Catoptrophorus semipalmatus*)	3	1	0	3	5	60
WHIM	Whimbrel (*Numenius phaeopus*)	0	0	0	6	0	16
HUGO	Hudsonian Godwit (*Limosa haemastica*)	0	0	0	3	10	51
MAGO	Marbled Godwit (*L. fedoa*)	0	3	0	2	13	9
WIPH	Wilson's Phalarope (*Phalaropus tricolor*)	216	621	356	1949	1895	2183
RNPH	Red-necked Phalarope (*P. lobatus*)	0	0	0	2	0	0
	All shorebirds	3246	3977	3601	6710	5477	5313
	Total of peak counts	6221	6185	5429	15,633	12,641	11,582
	Number of species	25	24	21	33	24	26

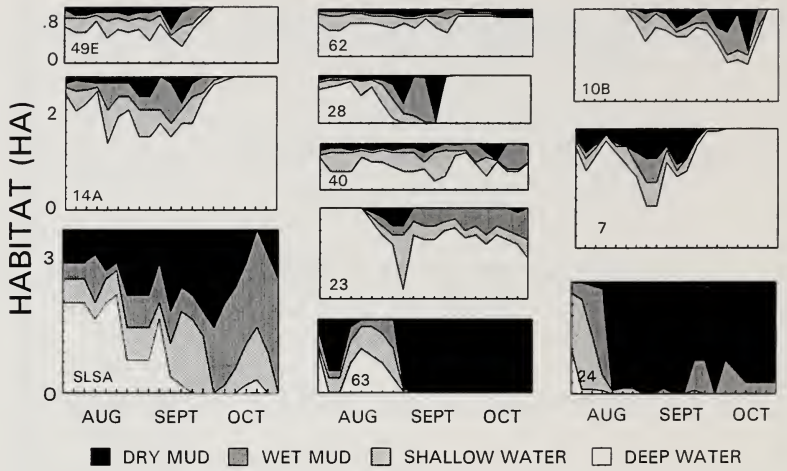


FIG. 2. Changes in availability of microhabitats (dry mud, wet mud, shallow water [<8 cm], and deep water [>8 cm]) in 11 wetlands through the late summer-fall migration season of 1990.

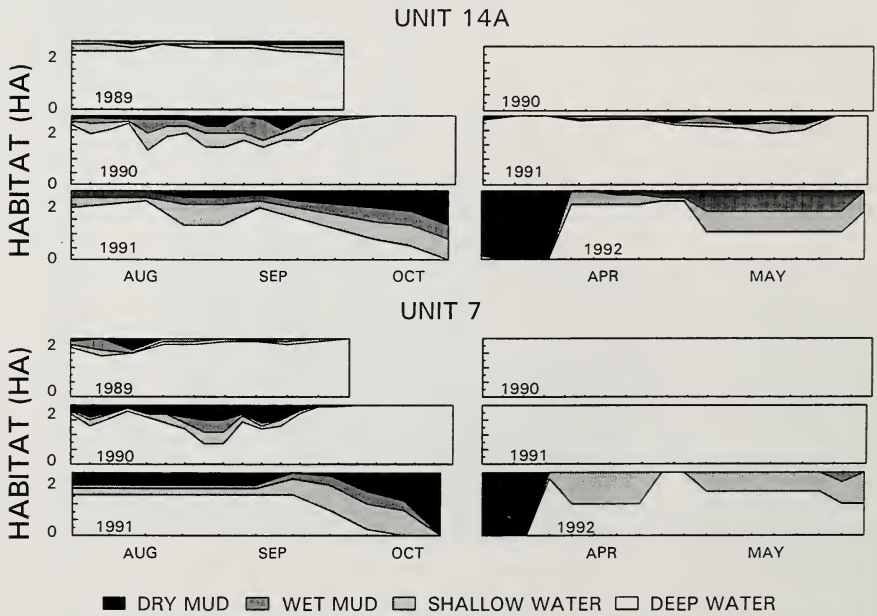


FIG. 3. Changes in availability of microhabitats (dry mud, wet mud, shallow water [<8 cm], and deep water [>8 cm]) in two wetlands throughout the six migration seasons of the study.

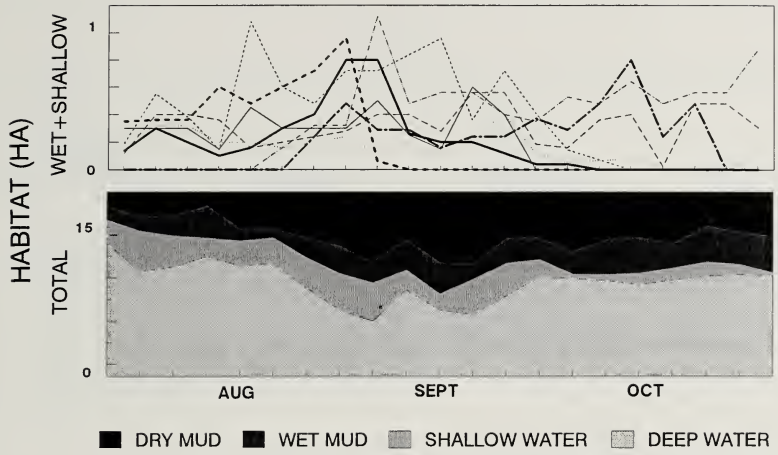


FIG. 4. (a) Amount of wet mud/shallow water (<8 cm) habitat in 11 wetlands through the 1990 fall season. (b) Total amount of wet mud/shallow water habitat across the 11 wetlands.

migration for 1–2 years, the first occurrence of wet mud/shallow water habitat coincided with the appearance of shorebirds (Table 2). As predicted, nearly all of the common species appeared in these wetlands once wet mud/shallow water habitat appeared, regardless of the recent wetland history.

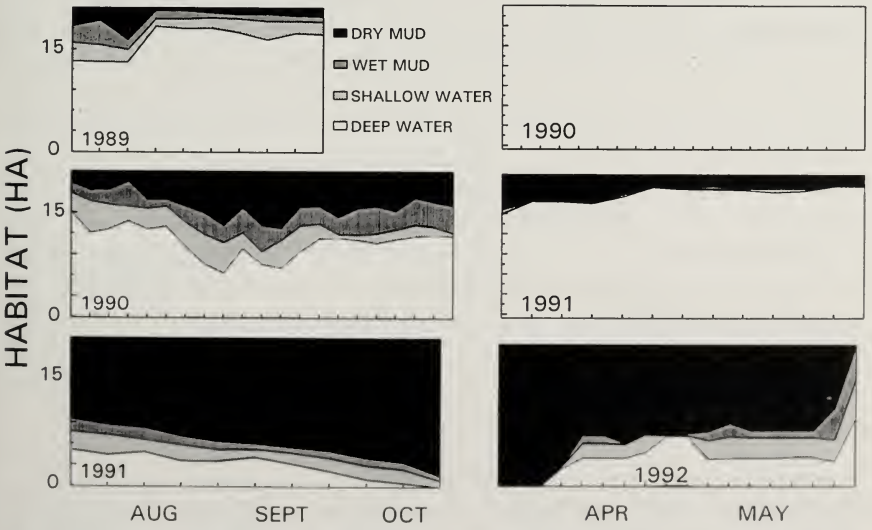


FIG. 5. Total amount of wet mud/shallow water habitat in 10 wetlands throughout the six migration seasons of the study.

TABLE 2

SHOREBIRD RESPONSES TO FIRST APPEARANCE OF WET MUD/SHALLOW WATER HABITAT WITHIN AND BETWEEN SEASONS IN SEVERAL WETLANDS

	Presence of shorebird species in wetland[a]								
	SESA	WESA	LESA	WRSA	BASA	GRYE	LEYE	STSA	LBDO
Within season[b]									
Fall 90 (N = 4)	−	+	−		+	−	+	+	+
Spring 91 (N = 5)	−		+	+	+	−	+	+	+
Spring 92 (N = 9)	−		−	+	+	+	+	−	+
Between seasons[b]									
Spring: no habitat available during two preceding springs (N = 4)	++		−	++	+	+	++	++	++
Spring: no habitat available during one preceding spring (N = 3)	++		+	++		+	++	++	++
Fall: no habitat available during one preceding fall (N = 9)	++	++	++		++	++	++	++	++

[a] Species codes as in Table 1. Within season: species present (+) or absent (−) at first appearance of wet mud/shallow water habitat. Between seasons: species present in ≥50% of wetlands (++); species present in 1–50% of wetlands (+); species in region but not present (−); blank cell indicates species not in region at time of survey.

[b] Wet mud/shallow water habitat first occurred in N wetlands during migration season.

Bird distribution relative to habitat.—We examined the relationship between numbers of birds and the amount of wet mud/shallow water habitat in wetlands on days selected according to total numbers of birds on the refuge and time in the season (see Methods). During spring, 71% of the selected wetland-days had no suitable habitat and no birds, 8% of

TABLE 3

RELATION BETWEEN NUMBERS OF SHOREBIRDS AND AREA OF WET MUD–SHALLOW WATER HABITAT DURING EIGHT FALL SURVEYS

Date	Number of wetlands	All shorebirds		Shorebirds associated with wet mud/shallow water	
		r	*P*[a]	*r*	*P*
14 Aug. 89	12	0.639	0.0125	0.615	0.017
31 Aug. 89	6	0.991	<0.0001	0.996	<0.0001
7 Sept. 89	7	0.982	<0.0001	0.977	<0.0001
10 Aug. 90	10	0.584	0.038	0.599	0.034
22 Aug. 90	11	0.723	0.006	0.720	0.006
4 Sept. 90	11	0.761	0.003	0.764	0.003
14 Sept. 90	11	0.300	0.370	0.360	0.138
26 Sept. 90	10	0.915	<0.0001	0.928	<0.0001

[a] *P* values are one-tailed.

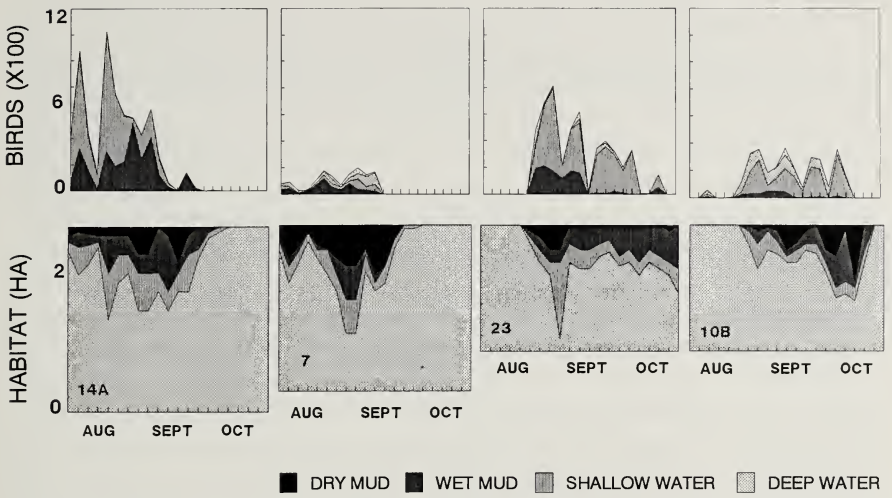


FIG. 6. Shorebird numbers associated with four microhabitats in four wetlands during the fall 1990 migration season.

the wetland-days had some available habitat but no birds, and 21% of the wetland-days had available habitat and some birds present (Fig. 6). In the late summer-fall seasons of 1989 and 1990, we found significant positive correlations between number of shorebirds and amount of wet mud/shallow water habitat on seven of eight selected days (Table 3). We were not able to quantify this trend during spring because there were not enough water units with wet mud/shallow water habitat to do so.

During six seasons of capturing and banding birds as part of a related study, we found limited evidence of individual birds returning to sites near where they had been originally banded. Of 2048 shorebirds captured between 1 Aug 1989 and 5 June 1992, five were recaptures of birds originally banded at Cheyenne Bottoms Wildlife Area (WA), Kansas, ca 30 km north of Quivira NWR. Four of these five were recaptured at Quivira NWR in subsequent seasons when shorebird habitat was unavailable at Cheyenne Bottoms WA (pers. obs., Table 4). In addition, one Semipalmated Sandpiper banded at Quivira NWR in the spring of 1990 was recaptured one year later (Table 4).

DISCUSSION

In the Great Plains, dramatic fluctuations in water levels are commonplace, transforming large deep lakes into mudflats or agricultural fields into expanses of sheet water. In the plains, wet mud/shallow water habitats are widely dispersed and highly unpredictable in space and time (Hands

TABLE 4
BANDING HISTORY OF SHOREBIRDS RECAPTURED AT QUIVIRA NATIONAL WILDLIFE REFUGE, KANSAS

Species	First capture		Recapture	
	Date	Location	Date	Habitat at Cheyenne Bottoms
Semipalmated Sandpiper[a]	28 May 90	Quivira NWR	11 May 91	—
Semipalmated Sandpiper[b]	19 Apr. 84	Cheyenne Bottoms	21 Apr. 90	Wet mud/ shallow water
Semipalmated Sandpiper[b]	30 Apr. 87	Cheyenne Bottoms	25 Apr. 92	Dry mud
Least Sandpiper[c]	25 Aug. 89	Cheyenne Bottoms	03 Aug. 90	Deep water
Semipalmated Sandpiper[c]	4 Aug. 90	Cheyenne Bottoms	08 Aug. 90	Deep water
Semipalmated Sandpiper[c]	25 Aug. 90	Cheyenne Bottoms	18 Sept. 91	Deep water

[a] Banded during this study.
[b] Banded by E. F. Martinez.
[c] Banded by G. Castro.

et al. 1991, Skagen and Knopf 1993). Even one of the largest and most stable wetlands in the central plains, Cheyenne Bottoms WA in central Kansas, suffers periodic drought and has no shorebird habitat during some migration times (Castro et al. 1990). The amount of wet mud/shallow water habitat is a complex function of many factors, including water level, topography of the wetland basin, wind action, and responses of vegetation and invertebrates to wetland conditions. Furthermore, water levels result from the combined effects of factors both extrinsic and intrinsic to a wetland, such as intentional water manipulation, local rainfall, surface runoff, stream flow, groundwater seepage (Kushlan 1989), elevation relative to water table, and type of underlying soil.

Our study indicates that shorebirds are capable of locating available habitat opportunistically. Island biogeographic theory proposes that during colonization of islands by dispersing species, these species will have a better chance at striking larger "targets" or finding larger habitats than small ones (MacArthur and Wilson 1967). Because the sizes of habitat islands (wetland patches) undergo rapid fluctuations, the strong correlation between numbers of birds and the size of suitable habitat patches is consistent with rapid colonization expected through opportunistic habitat use. On the other hand, if birds exhibited strong site faithfulness and water

levels fluctuated markedly, there would be little relation between amount of wet mud/shallow water habitat and numbers of shorebirds.

We also present evidence that shorebirds are capable of refueling in a specific wetland complex in consecutive years. In this study, however, we were not able to distinguish if the return of individuals occurred because habitat was available (opportunistic use) or if they intentionally returned to the same complex (site fidelity). If our birds exhibited site fidelity, the fidelity was to the larger wetland complex rather than to a particular wetland.

The interplay of habitat predictability and behavioral flexibility results in three general patterns of seasonal use of habitats, opportunistic use or colonization, traditional use, and site fidelity. Birds that exploit unpredictable resources in temporally dynamic wetlands probably rely on flexible behaviors such as opportunistic use or colonization behavior rather than fidelity to specific wetland sites (Colwell and Oring 1988). In fact, strong site fidelity to habitats that are unpredictable clearly would be maladaptive. Birds may exhibit greater site fidelity to habitats that are fairly predictable by nature, such as breeding habitats (Oring and Lank 1984, Gratto et al. 1985) or to habitats that are dynamic in a regular periodicity, such as intertidal areas (Smith and Houghton 1984). We propose that behavioral flexibility in shorebirds allows them to fine-tune resource exploitation over a broad range of habitat conditions, from the highly dynamic Great Plains wetlands to the relatively predictable coastal areas.

Clearly, a first step in conserving stopover habitats is the identification and preservation of the most predictable sites, as is underway within the Western Hemisphere Shorebird Reserve Network. In addition to specific site efforts, on the interior plains we see an urgent need for a coordinated regional approach that targets the maintenance of complexes of potential habitat to assure resource alternatives for migrating birds as local conditions vacillate (see also Reid et al. 1983). Conservation of interior-migrating shorebirds demands the availability of nearby alternative sites when traditional sites are lost (Castro et al. 1990, Smith et al. 1991). Wetland management practices that standardize water depths and fluctuations across wetland complexes generally preclude the very short-term wetland dynamics with which shorebirds evolved.

In this study, shorebirds responded to habitats at a fairly small geographic scale. At small spatial scales, however, wet mud/shallow water habitat may not always be present, and only at larger geographic scales may the effects of dramatic water fluctuations be modulated. Wide-ranging species such as migrating shorebirds are undoubtedly influenced by the regional juxtaposition of wetland complexes across the entire Great Plains.

We can compare dynamic wetlands to "shifting mosaics" of habitat patches (Bormann and Likens 1979, Baker 1989) as seen in forested ecosystems. Just as minimum sizes of nature reserves are hypothetically defined in terms of minimum land areas that exhibit stable patch mosaics (Baker 1989), the appropriate scale for managing continental stopover sites for shorebirds might be the number of wetlands that assures a high probability of suitable shorebird habitat regardless of weather regimes during migration.

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NEST BUILDING AND NESTING BEHAVIOR OF THE BROWN CACHOLOTE

Ana I. Nores and Manuel Nores[1]

Abstract.—We studied nesting behavior of the Brown Cacholote (*Pseudoseisura lophotes*) in Córdoba, Argentina from April 1989 to March 1993. Brown Cacholotes build many elaborate stick nests throughout the year and use each of them during the breeding period or for a short time in the non-breeding period. Nest building requires 15 to 37 days. Nests were usually built with thorny twigs, but the nature of the materials depends on availability. Usually each pair had several nests or part of them in their territory (range = 1–10). Nest building requires much of the birds' time and energy, but Brown Cacholotes generally use the material of old nests to minimize energy expenditure in nest construction. Both sexes shared all nesting activities. The birds copulate inside the nest, which is apparently unknown among birds. Egg laying occurred from last September to late February. Mean clutch size was 2.6 eggs (range = 2–4). The incubation period lasted 18–20 days and the nestling period 18–23 days. Nesting success was 59.3%, and an average of 1.5 nestlings were reared per clutch. Parental breeding experience, rather than age, would be more important influence on clutch-size and nesting success. Juveniles remained in the parental territories for 4–13 months. They contributed to nest building and defense of their territory, but their help was minimal. *Received 7 Dec. 1992, accepted 1 Sept. 1993.*

Although nest has been defined as a structure that aids the development of the eggs and the survival of young (Collias 1964), some birds build similar or different structures for use as dormitories throughout the year and have a close relation with them (Skutch 1961, Collias 1964, Welty 1979). This implies that nest-building behavior and nest structures are potentially under intense selective pressure. Because of this, detailed study of nest-building behavior can provide interesting clues to the evolutionary history and ecology of a species (Collias 1986).

The Brown Cacholote (*Pseudoseisura lophotes*) is a large bird (25 cm), with large feet, a strong bill, and a conspicuous crest. Its food consists mainly of insects and includes also seeds and eggs of various birds. This species inhabits savannas and woodlands in the Chaco region of northern and central Argentina, western Paraguay, and southern Bolivia (Short 1975). Its habitat also includes urban parks, squares, and gardens. It is a common bird with a conspicuous nest, but little has been published regarding its nest (see Masramón 1971, Vaurie 1980, Narosky et al. 1983, de la Peña 1987) and nothing about nest building and breeding behavior. We give here detailed information about nest characteristics, nest materials, nest sites, and construction. We report aspects of the breeding

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FIG. 1. Geographical location of the study areas: (1) Monte Cristo, (2) Córdoba Zoological Garden, (3) Santa Isabel.

behavior such as pair bonding, courtship, copulation, clutch size, incubation, development of nestlings, and nesting success.

STUDY AREA AND METHODS

We studied Brown Cacholotes for four years, from April 1989 to March 1993, at three sites in Córdoba province, Argentina. The main study site was located near the town of Monte Cristo (31°23′S, 63°53′W). This area (800 ha) is composed of cultivated land interspersed with remnant patches of xerophytic woodlands. Dominant tree species include *Prosopis nigra, Prosopis alba, Celtis spinosa, Geoffroea decorticans, Acacia* spp., *Capparis atamisquea,* etc. Additional observations were made at the Córdoba Zoological Garden (1 ha), where the Centro de Zoología Aplicada is located, and at sites (Santa Isabel, 25 ha) within Córdoba city (Fig. 1).

We studied 368 nests, 67 of which were breeding nests and 210 roosting nests, and there were 91 nests at the beginning of this study.

We used mist nets and a funnel trap (Martella et al. 1987) to catch the birds. We marked 211 individuals with leg bands of colored plastic and observed marked birds building 46 nests. We distinguished the sexes of individuals by observing copulation and egg-laying of

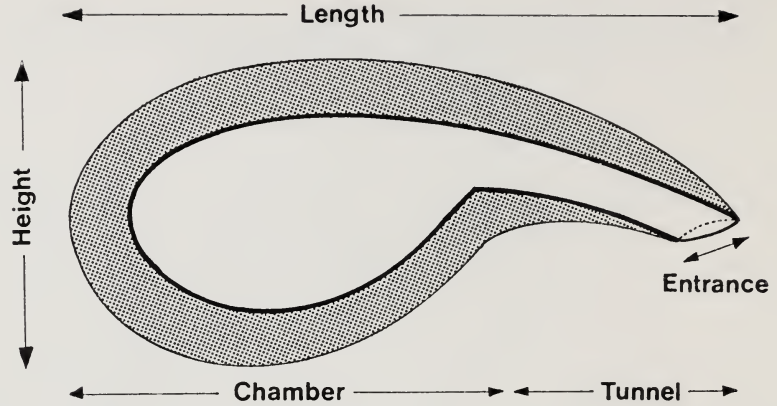

FIG. 2. Diagram of a longitudinal section through a Brown Cacholote's nest showing its components.

two and six banded birds, respectively. All nests built at 6 m or less above the ground were examined. To look into the nest, we opened a round hole in the brood chamber. After each examination, the hole was closed with oversized pieces of sponge following the procedure of Fraga (1980) and Mason (1985). Eggs were marked with waterproof ink, and the nestlings were marked with small, temporary rings from hatching until they were 10 days old. We visited the main study site every seven days during the non-breeding period and daily in the breeding period. We watched building daily in the Córdoba Zoological garden.

RESULTS

Nest sites.—Brown Cacholotes are strictly territorial. Usually, the territory of a cacholote pair contained several nests or remains of them ($\bar{x}$ = 4.4 ± [SD] 2.1 nests, range = 1–10). Nests were most frequently built in isolated trees, in trees in small clumps, or in those at the edges of cleared woodlands. Nests rarely were placed in dense woods (N = 7, 1.9% of total observed nests). The average height of the nests was 3.1 m above the ground (range = 1.60–17 m). In the study area, most nests were located among the lower branches of mesquites (*Prosopis* spp.), with twigs and branches of the trees incorporated in them. At the Córdoba Zoological Garden, the birds used various species of cultivated trees. The study areas contained many suitable nesting sites in trees. Nevertheless, in 92 cases (25%) cacholotes built a new structure upon an old nest.

Nest shape and size.—Brown Cacholotes build bulky nests consisting of two parts, a large oval chamber and a slightly down-curved entrance tunnel (Fig. 2). The average tunnel length is 30.1 cm ± 3.2 (range = 7–63) and its average inner diameter is 9.2 cm ± 1.1 (range = 9–10). At its inner end, it opens into a large chamber (inner diameter $\bar{x}$ = 22 cm ± 1.5, range = 19–24). The whole nest averages 90 cm in length (range =

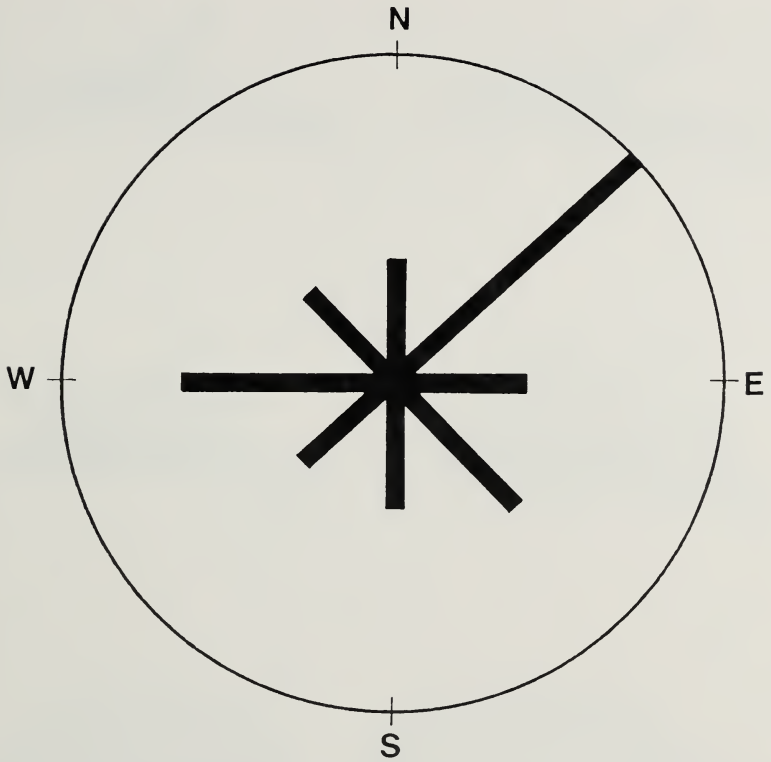

FIG. 3. Nest orientation of Brown Cacholote in trees (N = 120) Length of bars indicates number of nests that were found with an orientation toward each cardinal point: N (11), NE (29), E (12), SE (16), S (12), SW (11), W (18), NW (11).

60–125) and 43.3 cm (range = 32–55) in height. Nests weighed 2–5 kg. We counted 962 twigs in one small nest (2.5 kg) and estimate that large nests may contain as many as 2000 items. In general, the breeding nests ($\bar{x}$ = 100 cm ± 13.44) were larger than the roosting nests ($\bar{x}$ = 88 cm ± 10) (F = 46.05, df = 1,221, $P < 0.001$), and contained more twigs.

Cacholotes usually do not line the bottom of their nest chamber, and the eggs are laid directly on the twigs. Of 368 nests, only 11 (2.9%) were lined with a few fine sticks. The birds cut the thorns from sticks inside the chamber and tunnel. Although most nests were very compact, in some the cacholotes and their eggs could be seen through the wall.

The nests are oriented most commonly with their long axis facing NE (24%)(Chi square test χ^2 = 18.133, df = 6, $P < 0.01$)(Fig. 3).

Nest materials.—Most nests were composed of thorny twigs (twig length $\bar{x}$ = 15.6 cm ± 3.5, range = 9–75; twig diameter $\bar{x}$ = 5 mm ± 1.7, range

= 3–10). Where thorny twigs were unavailable, as in gardens and parks, the nest was built with thornless sticks. The kind of sticks in a nest usually varied. Those in the chamber were smaller and less often thorny, while the tunnel was made of larger, thornier pieces. The birds sometimes added other materials to their nests, including bits of wire (one nest contained 40% of them), small pieces of paper, plastic materials, and scraps of nylon. Nest material was collected, within 200 m of the nest, from trees, other nests, or the ground. After completion, breeding nests were often "adorned" with some long quill feathers of other birds, usually from Guira Cuckoos (*Guira guira*) and Chimango Caracaras (*Milvago chimango*).

Nest building.—Cacholotes require 15–37 days ($\bar{x} = 23 \pm 5.6$) to build their nests, but they continue to add sticks and repair them as long as they are in use.

Nests are built in the following sequence. First, both members of the pair carry sticks and twigs to a chosen branch until they form a small platform (Fig. 4A, B). This often takes a long time because the first sticks usually fall off the branch and wind often destroys the rudimentary structure. As soon as the platform is adequate, the birds begin to build up the nest wall to form a cup about 20 cm deep (Fig. 4C). Then, they begin the roof. When the chamber is partly covered, they start the entrance tunnel (Fig. 4D). When the tunnel is partly completed, they finish the chamber roof (Fig. 4E), and then they finish the tunnel (Fig. 4F).

Nests are built from the beginning, but often upon an old nest as foundation. Old nests are never reused for breeding or roosting. Birds build a roosting nest after they rear their young. In several cases, during the non-reproductive period, a pair finished building one nest and immediately began another. In two cases, birds destroyed a partly completed nest, using its materials to build another. Commonly, materials from old nests are used in new ones, especially those intended for breeding. Although some of the old nests are wholly demolished, a lot of them survive the years intact or partly demolished.

The birds spend much more time building a nest when they collect materials from trees or from the ground than from other nests ($F = 8.64$, $df = 1,10$, $P < 0.001$).

A Brown Cacholote pair sleeps in their nests throughout the year, but only for a short period in any one of them; ($\bar{x} = 42$, range = 5–55 days). During the pre-laying period, both members of the pair sleep together in the breeding nest. During egg-laying the female passes the night with the eggs, apparently incubating. The male usually roosts near the nest amid the foliage or in the penultimate nest, occasionally in the breeding nest. Juveniles remain in the parental territory, at first roosting in the nest where they were reared, later in their parent's new dormitory nest.

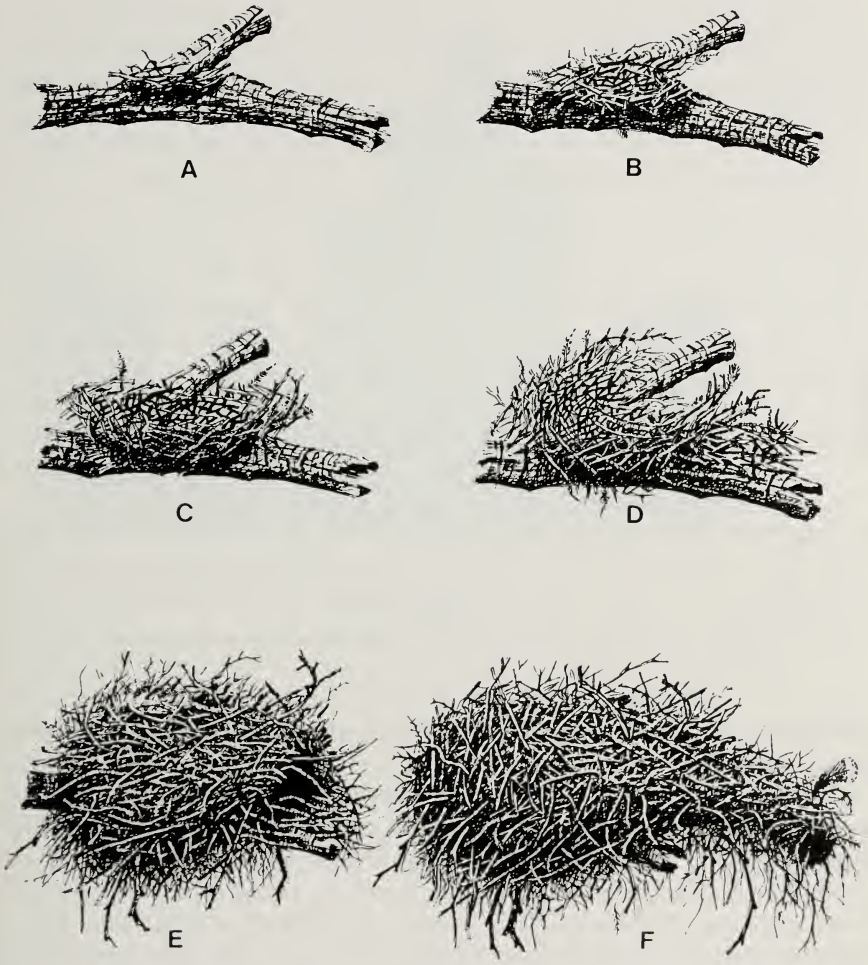

FIG. 4. Different stages in the construction of a Brown Cacholote's nest.

Cacholotes built 277 new nests over the four-year study period. A single pair built 17 nests in 36 months at the Córdoba Zoological Garden. The mean interval between the building of two nests was 62 days (range = 0–184). The birds built most actively just before the breeding season (Fig. 5). Morning and afternoon activity duration averaged 46% and 44.8% of the time (N = 86 h), respectively, and did not differ through the nest building period (ANOVA; $P > 0.05$). They interrupted their work at midday for approximately two hours. They relaxed their efforts by late afternoon, and stopped before sunset. Nest maintenance continued during

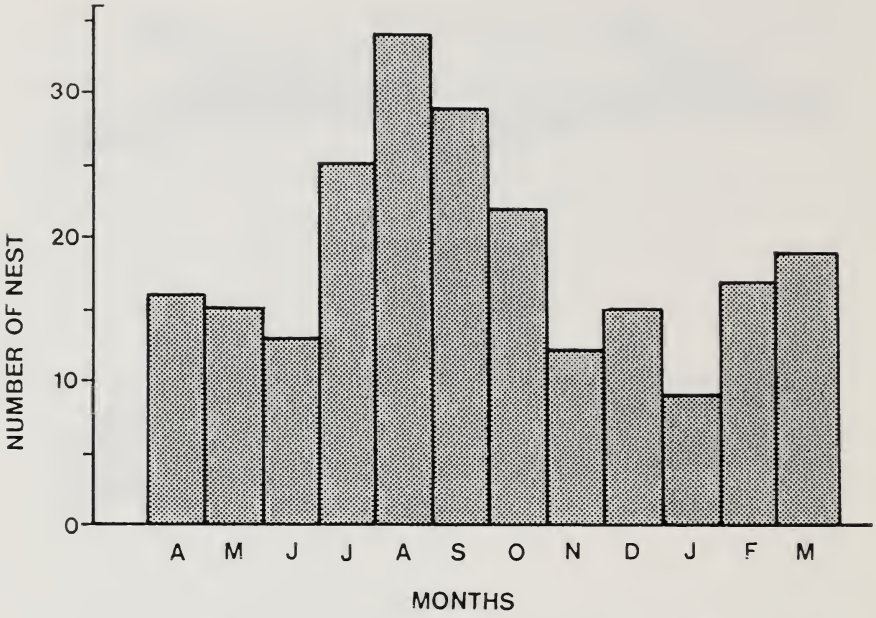

FIG. 5. Monthly frequencies of nest building by Brown Cacholotes.

the laying and the nestling period, especially the first days when the young were small.

During a 420-min period at one nest in the non-breeding season, a pair brought material 51 times; the male 26 times (51%), the female 22 (43%), while a juvenile collected three twigs (6%). During a 1920-min observation at another nest in the breeding season, the male brought 62 twigs and the female 24. At a different nest, a juvenile carried three twigs (4% of the total number brought to this nest, during 1200 min of observation).

Pair bond.—Brown Cacholotes are monogamous; they remain paired throughout the year and for consecutive breeding seasons. Four pairs were mated throughout the four study years, eight pairs for three years, and 13 pairs for two years. When a bird died, the survivor of the pair promptly found a new partner. We observed two banded birds who changed mates during the breeding season. One female who lost her mate in the second week of September had acquired another (banded) by the first week of October. In a second case, a male who lost his mate during the first days of December had mated with an unbanded female by the second week of the same month.

Courtship and copulation.—Courtship displays are given almost exclusively by the male cacholote, near and inside the nest, as we could see in

some nests with thinner walls. The display begins when both birds are near the nest. After they repeatedly sing in duet, the male, with his body nearly horizontal, bristles his feathers, spreads and elevates his tail, droops his wings until they nearly touch the floor, depresses his bill, and utters a series of short notes at a rate of about two per second. He enters the nest. The watching female enters the tunnel where she remains for a few seconds while the male, maintaining the same posture, rotates his body two or three times in the chamber, stopping with his bill toward her. Then the female joins him in the nest chamber and crouches low for about 15 sec. With feathers still erect, the male advances towards her. He circles around her and mounts her, depressing his tail while she elevates hers. After copulation, the birds sing a duet inside their nest. We observed this behavior four times in the pre-laying and the egg-laying periods. Similar displays were observed when the pair started to build a breeding nest, but they did not copulate on these occasions.

Egg-laying.—Mean clutch initiation date was 19 November (range = 25 Sept.–14 Jan.). Throughout the study, seven replacement clutches were laid from mid-December to late January. In every case, the nests were preyed upon, and the cacholotes built new nests. Most of the eggs were deposited with an interval of two days (N = 177, range = 1–3). Two-day laying intervals are usual in furnariids (Skutch 1969, Fraga 1980).

Clutch size.—Brown Cacholotes lay two or three eggs, rarely four. The mean clutch size was 2.6 eggs. Older pairs had larger clutches ($\bar{x}$ = 3.2 eggs, N = 34, range = 2–4) than younger pairs ($\bar{x}$ = 2.2, N = 16, range = 2–3)(Mann-Whitney test, $Z = 4.55$, $P = 0.001$). There was no significant difference in clutch-size among the first-time breeders of different age.

Egg measurements.—The average length and diameter of 135 eggs was 27.1 ± 0.4 mm (range = 25.5–29.1) and 20.8 ± 0.5 mm (19.1–21.5). Differences in egg size between females with previous breeding experience and first-time breeders were not significant (Mann-Whitney test; $Z = 1.08$, $P = 0.27$). The mean weight was 7.6 ± 0.5 g (6.8–8.5). Frequently, the eggs were stained with blood.

Incubation.—The incubation period was 18 to 20 days ($\bar{x}$ = 18.6). Both parents incubated in daytime, but only the female at night. Sessions on the eggs were 5–35 min ($\bar{x}$ = 28), and the longest period of neglect was 30 min. The sexes incubated with equal constancy. The male usually entered the nest soon after the female left and remained until she returned.

Second broods.—Second broods were found in only four of 67 nests examined (5.9%). In all cases the pairs built a new nest. The intervals between the departure of the last young of the first brood and the laying of the first egg of the second set were 106, 98, 89, and 74 days, respectively.

Nestling period.—Male and female cacholotes spent equal time and

energy during the nestling period and made similar contributions to feeding the nestlings. During the first days, females devoted 45.8% (5 trips/h) and males 46.0% (4 trips/h) of the hours of observation (N = 19 h) to feeding them. During the second week, the females and males spent 65.8 and 63.3%, respectively (N = 17 h), bringing 9 and 12.5 items/h. During the last week of nestling life, the pair increased the time of feeding to 72 and 73%, respectively, and brought 18 and 19.6 items/h (N = 21 h). After the young fledged, the parents continued to feed them freely for about 20 more days, then gradually reduced the number of meals. Although young cacholotes continued to beg their parents for food for 36–40 days after leaving the nest, they were ignored. Both parents brooded the nestlings in daytime but usually only the female at night. The time spent in brooding gradually decreases through the nestling period. Both sexes carried away the egg shells and fecal sacs.

Development of nestlings.—The mean mass of the newly-hatched cacholotes was 5.7 g (SD = 1.2 g, N = 98). The mouth lining is grayish-yellow and the flanges are pale yellow. They have gray plumule on the head, wings, and dorsal flanks. The nestlings' eyes begin to open at days 4–5, but until day 10 they are closed most of the time. Feather tracts become visible as darker lines on the skin at days 3–4. Pinfeathers visibly project from the skin at days 5–6. The first feather tips are seen on day 7 in the pinfeathers of the dorsal tracts. By day 10–11, most of the pinfeathers are visible except those of the capital tract. At this time, nestlings have conspicuous yellow oral flanges, pale gray feet, and grayish bills. The eyes are bluish-gray or greenish-gray. Wing flapping was observed at day 9. Nestlings are almost completely feathered at day 17. When the young fledge, they are well feathered, but the tail and crest are still quite short. The growth of the nestling shows a typical sigmoidal curve (Fig. 6). At first slow, growth accelerates until the young weigh about 80 g. Young cacholotes are about as heavy as adults when they leave the nest. The mean nestling period is 19 ± 2.3 days (range = 18–23 days).

Departure and dispersion of the juveniles.—The young remained in the parental territory five to 13 months. Parents were more intolerant of young males than of young females; consequently, the latter remained longer with their parents ($\bar{x}$ = 245.3 days ± 35, N = 14, range = 198–414) than the males ($\bar{x}$ = 65 days ± 27, N = 16, range = 60–256) (Mann-Whitney test; $Z = 2.45$, $P = 0.05$). They often defended the parental nests. When the parents were present, the juveniles were not allowed to help with nest construction and were often chased from the nest. Nestlings about to leave the nest frequently answer parental calls and may even attempt to duet with a parent or siblings.

After departure, 42 (40%) of the fledglings occupied new areas near the

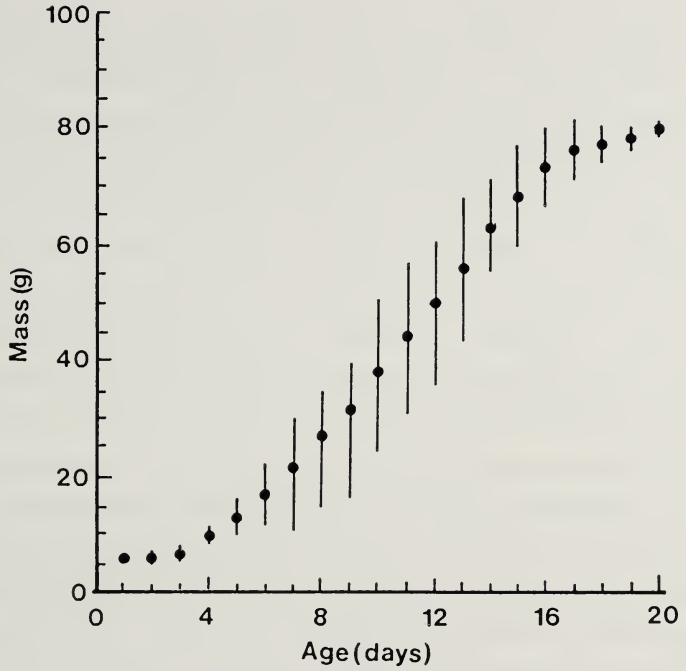

FIG. 6. Masses of nestling Brown Cacholotes.

parental territories when they built their first nests after they mated. The average distance between a young birds' nest and an active parent's nest was 120 m (range 98–1300). The other fledglings disappeared from the study area. Of the 105 juveniles fledged during the four-year study period, 42 (40%) mated and reared fledglings. Nine (21.4%) were one-year-old birds, 22 (52.3%) two years old, and 11 (26.1%) three years old.

Nesting success.—Of 177 eggs laid in 67 clutches, 144 eggs hatched (81.3%). Losses were attributed to failure to hatch (N = 10, 30.3%) and predation by white-eared opossums (*Didelphis albiventris*)(N = 8, 24.2%), rats (*Rattus rattus*) (N = 7, 21.2%), and various birds (N = 6, 18.1%). The losses due to manipulation by us were minimal (N = 2, 6.1%). Of the 144 nestlings, 105 fledged (fledgling success: 72.9%). Most of the losses were death in the nest (N = 12, 30.7%) and predation (N = 24, 61.5%). On four occasions, nests were attacked and occupied by white-eared opossums. Twice nests were preyed upon by rats. Both predators were common in the study area and were observed inside the nest chamber.

Nesting success of older experienced pairs was significantly higher than that of first-time breeders (Mann-Whitney test; $Z = 3.68$, $P = 0.002$). Juveniles with previous breeding experience have significantly higher nest-

ing success than those of the same age without experience (Mann-Whitney test; $Z = 5.32$, $P = 0.003$). The over-all nesting success was 59.3%. An average of 1.5 (range = 1–3) fledglings were reared per clutch.

Secondary tenants.—Paper wasps occupied 56 of the 368 nests (15.2%) in the autumn, 42 (75%) of these by *Polybia occidentalis* and 14 (25%) by *Polistes canadensis,* (Vespidae, Hymenoptera). Wasps built honeycombs in the nest chamber, in the nest tunnel, or under the nest. Eighty percent of all nests occupied by *Polybia occidentalis* were active, whereas only 15% of all nests occupied by *P. canadensis* were active. Occupation of an active nest by any species of paper wasp caused cacholotes to abandon it. Ants of the genus *Camponotus* occupied eight (2.1%) abandoned nests. Large numbers of other arthropods (Arachnidae, Reduviidae, Cimicidae, Chrysomelidae, Coccinelidae), use Brown Cacholote nests, mainly to hibernate.

On nine occasions (2.4%) Monk Parakeets (*Myiopsitta monachus*) chose abandoned or occupied nests as winter roosts or for breeding in the spring. In every case, the parakeets remodeled the nest, extending the entrance tunnel with thorny twigs. Once (0.2%) a Tropical Screech-Owl (*Otus choliba*) slept in an abandoned nest in December. Bay-winged Cowbirds (*Molothrus badius*) used 14 (3.8%) abandoned and two active nests (0.5%) for breeding in January and February. Cacholotes relinquished both nests and started new ones. A cacholote nest with one egg was parasitized by a Shiny Cowbird (*Molothrus bonariensis*) on 19 January 1991. By the next day, the cowbird's egg had disappeared and a second egg of the cacholote had been laid. House Sparrows (*Passer domesticus*) bred in four (1%) abandoned cacholote nests. Frequently they pilfer feathers and shreds of nylon from active and abandoned nests. Once Cattle Tyrants (*Machetornis rixosus*) and twice White Monjitas (*Xolmis irupero*) and Saffron Finches (*Sicalis flaveola*) selected deserted cacholotes' nests for breeding.

Mammals also occupy nests of Brown Cacholotes. During the winter, we found two rats (*Rattus* sp.) inside a newly built nest. The birds abandoned this nest and started to build a new one. Once we found a mouse (Cricetidae) with three young in a nest with two cacholote's eggs. The eggs disappeared and the birds abandoned the nest.

White-eared opossums occupied five deserted cacholotes' nests and one active nest. Probably the birds were preyed upon by the opossum because they disappeared from the area.

DISCUSSION

The Brown Cacholote is monomorphic, and male and female live together in the same territory throughout the year. Both members of a pair

build and repair nests. The young remain with their parents until the next breeding season, so that the birds are found in pairs but more frequently in families of four or five individuals. Similar results are also observed in the White-throated Cacholote (*Pseudoseisura gutturalis*) (Hudson 1920).

Brown Cacholotes build several nests throughout the year and use them for breeding and sleeping. According to Skutch's (1961) dormitory classification, the Brown Cacholote falls into category 2 d: nests are occupied by parents and self-supporting young throughout the year. Also in this category is the Firewood-gatherer (*Anumbius annumbi*), a sympatric species, which likewise builds elaborate nests of thorny twigs.

Increasingly, evidence indicates that heavy infestation of nests by ectoparasites affects the survival and fecundity of breeding adult birds (Clark and Mason 1988) and causes the death of nestlings (Ricklefs 1969). The use of a nest for only one breeding season (Clark and Mason 1988), and for a short period during the nonreproductive season reduces the time during which ectoparasites multiply in it. These strategies are used by cacholotes and could diminish infestation by ectoparasites. Some authors suggest that some birds use green material with secondary compounds in their nests to repel or kill avian ectoparasites (Wimberger 1984; Clark and Mason 1985, 1988; Bucher 1988). The Brown Cacholote does not line its nests with green material, but it uses the nest for a short time. It differs from the Firewood-gatherer, which lines its nests with green plants but usually occupies it for two breeding seasons (Nores and Nores unpubl. data).

The long entrance tunnel and thorny materials like those found in the Brown Cacholote's nests have been considered as probable elements to deter predators, especially snakes and mammals (Collias 1964, 1986). The nest location among the lower branches of mesquite trees could reduce its detection by avian predators. The nest interstices permit birds inside to see through the walls and fly away when an intruder approaches (Skutch 1969, Thomas 1983). All nests in this study contained only one entrance tunnel, but de la Peña (1987) mentioned a nest with two.

The different materials used in nest construction reflect differences in their availability. Although cacholotes usually build with thorny sticks, they can complete a nest with thornless twigs, sometimes with the addition of other materials such as bits of wire and plastic materials.

Some birds use methods that reduce the energetic cost of nest construction (Mountjoy and Robertson 1988). Brown Cacholotes take material from their old nests to build new ones. Those close to the new site are convenient sources. This procedure reduces the large expenditure of time and energy required to procure nest materials, especially for breeding nests.

Other animals frequently occupy cacholote nests as safe sites for roosting, hibernating, or breeding. Thus the nests play an important role in the Chaco ecosystem.

In our study, the laying period was from September to February. This period was longer than that reported by Narosky et al. (1983) and de la Peña (1987), who recorded egg-laying only from September to December.

The Brown Cacholote copulates and does part of the courtship inside the nest chamber. This fact is apparently unknown among birds, but it may occur in the Sociable Weaver (*Philetairus socius*)(Collias and Collias 1978).

Fraga (1980) studied the Rufous Hornero (*Furnarius rufus*), a sympatric ovenbird, which builds elaborate nests of mud or clay. This species and the Brown Cacholote nested with different success. Fraga pointed out that the combination of low mortality and high productivity found in Rufous Horneros is unusual among local birds. The Brown Cacholotes' productivity was lower; 1.5 vs 2.52 fledglings per clutch. The clutch size was also lower; 2.60 in cacholote vs 3.35 in hornero.

Among factors which may control clutch-size and nesting success in birds, the role of parental age and breeding experience has received much attention (Perrins and McCleery 1985, Buitron 1988, Lequette and Weimerskirch 1990, Goodburn 1991, Croxall et al. 1992). Older and more experienced Brown Cacholotes had significantly larger clutches and higher nesting success than first-time breeders. Because this species begins breeding over an age range of 1–3 years, individuals of the same age can have variation in breeding experience. This provides a framework for analyzing the influence of age and experience separately. First-time breeders of different age did not differ significantly in these two variables. Juveniles with breeding experience had significantly larger clutches and higher nesting success than those of the same age without breeding experience. This suggests that experience, rather than age, is the more important influence on clutch-size and nesting success in the Brown Cacholote.

The last nestlings in broods of three usually died as did all in broods of four, probably of starvation. In the cases where these last-hatched nestlings survived, they were underweight.

The young remain in the parental territory for many months after they become self-supporting. They occasionally help their parents to defend their territory and bring sticks and adjust them in the nest. The birth-to-breeding distance is short ($\bar{x}$ = 120 m). These characteristics may be considered a step toward cooperative breeding. According to the classification of avian communal systems (Brown 1978), the Brown Cacholote might be included in TSD (territorial, single breeding, delayed breeding).

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A GLOSSARY FOR AVIAN CONSERVATION BIOLOGY

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ABSTRACT.—This glossary provides standard definitions for many of the terms used in avian conservation biology. We compiled these definitions to assist communication among researchers, managers, and others involved in the Neotropical Migratory Bird Conservation Program, also known as Partners in Flight. We used existing glossaries and recent literature to prepare this glossary. The cited sources were not necessarily the first ones to use the terms. Many definitions were taken verbatim from the cited source material. Others were modified slightly to clarify the meaning. Definitions that were modified to a greater extent are indicated as being adapted from the originals. Terms that have been used in more than one way by different authors are listed with numbered alternative definitions if the definitions differ substantially. *Received 30 March 1993, accepted 23 July 1993.*

GLOSSARY

Accuracy: the closeness of computations or estimates to the exact or true value (Marriott 1990:2).

After-hatching-year (AHY) bird: a bird in at least its second calendar year of life (Pyle et al. 1987:27; Canadian Wildlife Service and U.S. Fish and Wildlife Service 1991:5–47).

After-second-year (ASY) bird: a bird in at least its third calendar year of life (Pyle et al. 1987:27; Canadian Wildlife Service and U.S. Fish and Wildlife Service 1991:5–47).

After-third-year (ATY) bird: a bird in at least its fourth calendar year of life (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1991:5–47).

Allopatric: occurring in different places; usually refers to geographical separation of populations (Ricklefs 1979:865). The populations may exhibit divergence in behavior, morphology, or genetic composition.

Annual: referring to an organism that completes its life cycle from birth or germination to death within a year (Ricklefs 1979:865).

Area-sensitive species: species that respond negatively to decreasing habitat patch size (Finch 1991:20).

Assemblage: a set of organisms whose pattern of organization (with respect to competition, predation, mutualism, etc.) is unknown (Giller and Gee 1987:537) (cf Community).

Assessment endpoint: see Endpoint.

Association: a group of species living in the same place at the same time (Ricklefs 1979: 865).

Atlas: the result of a comprehensive survey of a large geographical area that maps the occurrence (or occurrence and relative abundance) of species in subdivisions of that area. An atlas is usually based on a grid of fixed intervals of distance or degrees latitude and longitude. It is restricted to a particular season of the year, usually the breeding season (Ralph 1981:577).

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Biodiversity: (1) the variety of life forms, the ecological roles they perform, and the genetic diversity they contain (Wilcox 1984:640); (2) the variety from molecular, population, and interspecific levels up to the heterogeneity of ecosystems and landscapes (Hansen and diCastri 1992:5) (syn. biological diversity).

Biogeography: the study of the geographic distributions of organisms, both past and present (Brown and Gibson 1983:557).

Biological species concept: the idea that species are groups of natural populations that are reproductively isolated from other such groups (McKitrick and Zink 1988:2) (cf Phylogenetic species concept).

Biomarker: the variation, induced by a substance foreign to the body, in cellular or biochemical components or processes, structures, or functions that is measurable in a biological system or sample (McCarthy et al. 1991:2).

Boundary: the edge between different habitat types. If distinctive, a boundary can be considered a separate edge habitat or ecotone. Boundaries that are readily crossed by an organism are called permeable, those that are crossed reluctantly are called semipermeable, and those that are not crossed are called impermeable (Dunning et al. 1992:173).

Breeding Bird Atlas: see Atlas.

Breeding Bird Census (BBC): a census program of the National Audubon Society in North America that uses the spot-mapping method during the breeding season (Ralph 1981: 577).

Breeding Bird Survey (BBS): a cooperative program of the U.S. Fish and Wildlife Service and the Canadian Wildlife Service for monitoring population changes in North American breeding birds by using point counts along roads (Ralph 1981:577).

Breeding dispersal: movement of individuals that have reproduced between successive breeding sites (Greenwood 1980:1141).

Brood parasitism (interspecific): the laying of eggs by an individual of one species in nests of other species with subsequent care for the parasite young provided by the hosts (Lanyon 1992:77) (syn. breeding parasitism, nest parasitism [Thomson 1964:594]).

Capture-recapture method: a procedure involving the distinctive marking of individuals and their subsequent recapture (or sighting) to estimate population size and other population parameters (Ralph 1981:577) (syn. mark-recapture).

Carrying capacity: the maximum number of individuals that can use a given area of habitat without degrading the habitat and without causing social stresses that result in population reduction (McNeely et al. 1990:153).

Catastrophe: an event that causes sudden decreases of population size or the entire elimination of subpopulations (Ewens et al. 1987:62).

Census (noun): a count of all individuals in a specified area over a specified time interval (Ralph 1981:577).

Census (verb): the act or process of counting all individuals within a specified area and estimating density or a total population for that area (Ralph 1981:577).

Census efficiency: proportion of actual population density that is assessed by a census (Ralph 1981:577) (cf Detectability).

Christmas Bird Count (formerly "Census") (CBC): an annual project, in the Americas, of the National Audubon Society involving a one-day count in December of the individuals of all species observed within a circle that is 15 miles (24 km) in diameter (Ralph 1981: 577).

CITES species: species (675 as of this writing) listed under the 1975 Convention on International Trade in Endangered Species (CITES), which is administered by the United Nations Environment Programme. Such species cannot be commercially traded as live specimens or wildlife products because they are endangered or threatened with extinction (Miller 1992:422).

Climate change: changes in the global climate system in response to physical feedbacks, chemical feedbacks, and changes in terrestrial and aquatic systems caused by humans and nature (adapted from Lubchenco et al. 1991).

Climax: the endpoint of a successional sequence; a community that has reached a steady state under a particular set of environmental conditions (Ricklefs 1979:867).

Cline: a geographic gradient in a measurable character, or gradient in gene, genotype, or phenotype frequency (Endler 1977:180).

Coarse-grained: referring to qualities of the environment that occur in large patches with respect to the activity patterns of an organism. This results in the organism's ability to select usefully from among qualities (Ricklefs 1979:867) (cf Fine-grained).

Common Birds Census (U.K.) (CBC): a program of the British Trust for Ornithology for censusing breeding birds using the spot-mapping method (Ralph 1981:577).

Community: a group of organisms, generally of wide taxonomic affinities, occurring together. Many will interact within a framework of horizontal and vertical linkages such as competition, predation, and mutualism (Giller and Gee 1987:539) (cf Assemblage).

Competition: an interaction between members of two or more species that, as a consequence either of exploitation of a shared resource or of interference related to that resource, has a negative effect on fitness-related characteristics of at least one of the species (Wiens 1989b:7–8).

Connectedness: the structural links between habitat patches in a landscape; can be described from mappable features (adapted from Baudry and Merriam 1988:23).

Connectivity: a parameter of landscape function that measures the processes by which a set of populations are interconnected into a metapopulation (adapted from Baudry and Merriam 1988:23).

Constant-effort mist netting: a capture method, standardized over space and time, used for counting numbers of birds captured in mist nets (Ralph et al., in press).

Contact: a single field record of an individual by sight or sound (Ralph 1981:577) (syn. detection, cue, registration, observation).

Corridor: a spatial linkage that facilitates movements of organisms among habitat patches in a landscape (adapted from Merriam 1988:16).

Count (noun): (1) the act or process of enumerating; (2) the number or sum total obtained by counting (Ralph 1981:577).

Count (verb): to record the number of individuals or groups present in a population or population sample (Ralph 1981:577) (cf Census, Index).

Deforestation: removal of trees from a forested area without adequate replanting or natural regeneration (Miller 1991:A6).

Demographic parameters: fecundity and mortality parameters used to predict population changes, such as number of eggs laid per clutch, the frequency at which clutches are laid, the survivorship of eggs and young in the nest and to the age at first reproduction, and the subsequent survival of the adults throughout their lifetime (Ricklefs 1972:367).

Density: the number of units (e.g., individuals, pairs, groups, nests) per unit area (Ralph 1981:577) (cf Frequency).

Density-dependent: having influence on individuals in a population in a manner that varies with the degree of crowding in the population (Ricklefs 1979:868).

Density-independent: having influence on individuals in a population in a manner that does not vary with the degree of crowding in the population (Ricklefs 1979:868).

Detectability: a measure of the conspicuousness of a species equal to the proportion of actual units (individuals, territorial males, etc.) observed on a given area (Ralph 1981:577).

Detection distance: the distance from the observer at which the individual or cluster of individuals is seen or heard (the radius in point counts and the lateral or perpendicular distance in transect counts) (Ralph 1981:577–578).

Direct competition: the exclusion of individuals from resources by aggressive behavior or use of toxins (Ricklefs 1979:868).

Dispersal: the movement of organisms away from the place of birth or from centers of population density (Ricklefs 1979:868) (see Breeding dispersal, Natal dispersal).

Dispersion: (1) the pattern of spacing of individuals in a population (Ricklefs 1979:868); (2) the nonaccidental movement of individuals into or out of an area or population, typically a movement over a relatively short distance and of a regular nature (Lincoln et al. 1982:70).

Disturbance: any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (Turner 1989:181).

Diversity: typically used in relation to species, a single index that incorporates the number of species and relative abundances of species (evenness). For example, a collection is said to have high diversity if it has many species and their abundances are relatively even. There are many types of diversity (Pielou 1977:292; Wiens 1989a:123):

Point diversity—for a small or microhabitat sample within a community regarded as homogeneous

Pattern diversity—as change between parts of the internal pattern of a community

Alpha diversity—for a sample representing a community regarded as homogeneous (despite its internal pattern)

Beta diversity—as change along an environmental gradient or among the different communities of a landscape

Gamma diversity—for a landscape or set of samples including more than one kind of community

Delta diversity—as change along climatic gradients or among geographic areas

Epsilon diversity—for a broader geographic area, including differing landscapes.

Ecocline: a geographical gradient of vegetation structure associated with one or more environmental variables (Ricklefs 1979:868).

Ecological effects characterization: the identification and quantification of the adverse effects elicited by a stressor and, to the extent possible, the evaluation of cause-and-effect relations (Risk Assessment Forum 1992:5).

Ecological risk assessment: a process that evaluates the likelihood that adverse ecological effects may occur or are occurring as a result of exposure to one or more stressors. Ecological risk assessment may evaluate one or many stressors and ecological components (Risk Assessment Forum 1992:2).

Ecological risk characterization: a process that uses the results of the exposure and ecological effects analyses to evaluate the likelihood of adverse ecological effects associated with exposure to a stressor (Risk Assessment Forum 1992:5).

Ecosystem: the totality of components of all kinds that make up a particular environment; the complex of biotic community and its abiotic, physical environment (McNeely et al. 1990:153).

Ecotone: a habitat created by the juxtaposition of distinctly different habitats; an edge habitat; a zone of transition between habitats types (Ricklefs 1979:869) or adjacent ecological systems having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions (Hansen and diCastri 1992:6) (see Boundary).

Edge effect: (1) changes in a community due to the rapid creation of abrupt edges in large units of previously undisturbed habitat (Reese and Ratti 1988:127); (2) tendency for increased variety and density of organisms at community or habitat junctions (Odum 1971:157).

Edge species: species preferring the habitat created by the abutment of distinctive vegetation types (Ricklefs 1979:869).

Endangered Species Act: 1973 Act of U.S. Congress, amended several times subsequently, that elevates the goal of conservation of listed species above virtually all other considerations. The act provides for identifying (listing) endangered and threatened species or distinct segments of species, monitoring candidate species, designating critical habitat, preparing recovery plans, consulting by federal agencies to ensure that their actions do not jeopardize the continued existence of listed species or adversely modify critical habitats, restricting importation and trade in endangered species or products made from them, restricting the taking of endangered fish and wildlife. The act also provides for cooperation between the federal government and the states (adapted from Rohlf 1989:25–35).

Endemic: confined and native to a certain region (Ricklefs 1979:869).

Endpoint: a characteristic of an ecological component that may be affected by exposure to a stressor (Risk Assessment Forum 1992:12); a characteristic of valued environmental entities that are believed to be at risk (Suter 1990:9). Suter (1990) distinguished two types of endpoints:

Assessment endpoint—an explicit expression of the actual environmental value that is to be protected (Suter 1990:9)

Measurement endpoint—a measurable response to a stressor that is related to the valued characteristics chosen as the assessment endpoints (Suter 1990:10).

Environment: physical and biological surroundings of an organism, including the plants and animals with which it interacts (Ricklefs 1979:869).

Environmental characterization: the prediction or measurement of the spatial and temporal distribution of a stressor and its co-occurrence or contact with the ecological components of concern (Risk Assessment Forum 1992:5).

Environmental gradient: a continuum of conditions, such as the gradation from hot to cold environments (Ricklefs 1979:869).

Equitability: (1) evenness relative to any specific standard or model of species abundance (Peet 1974:288); (2) uniformity of abundance in an assemblage of species. Equitability is greatest when all species are equally numerous (Ricklefs 1979:869) (syn. evenness).

Estimator: a function of sample data that describes or approximates a parameter (Ralph 1981:578).

Evenness: the uniformity of abundance between species in a community (Peet 1974:288).

Exploitation: the removal of individuals or biomass from a population by predators or parasites (Ricklefs 1979:870).

Exploitation competition: competition in which two or more organisms consume the same limited resource (Ehrlich and Roughgarden 1987:620) (cf Interference competition).

Extinction: (1) the complete disappearance of a species from the earth (Miller 1991:A5); (2) the total disappearance of a species from an island (this does not preclude later recolonization) (MacArthur and Wilson 1967:187) (cf Extirpation, Local extinction).

Extirpation: the elimination of a species from an island, local area, or region.

Extractive reserves: conservation areas that permit certain kinds of resource harvesting on a (theoretically) sustainable basis (Soulé 1991:747).

Fecundity: rate at which an individual produces offspring, usually expressed only for females (Ricklefs 1979:870).

Feral: escaped from domestication (Long 1981:7). Feral individuals may be descendants of the original escapees.

Fine-grained: referring to qualities of the environment that occur in small patches with respect to the activity patterns of an organism. This results in the organism's inability to distinguish qualities usefully (Ricklefs 1979:870) (cf Coarse-grained).

First-year bird: a bird in its first 12–16 months (or until its second prebasic molt) (Pyle et al. 1987:27) (see Hatching-year bird, After-hatching-year bird).

Fitness: the average contribution of one allele (i.e., one form of a gene) or genotype to the

next generation or to succeeding generations, compared with that of other alleles or genotypes (Futuyma 1979:503). It may be either an absolute value, measured by the number of progeny per parent, or it may be relative to some reference genotype (Crow and Kimura 1970:224).

Fixed-distance method: see Strip transect method, Point count method.

Fledging success: (1) the average number of offspring fledged (i.e., raised until they leave the nest) per female (May and Robinson 1985); (2) percentage of hatchlings that fledge (Robinson and Rotenberry 1991:280).

Floating birds: reserves of nonbreeding or nonterritorial birds, usually of undetermined age, present in breeding or territorial populations (von Haartman 1951:433–435).

Floristic: referring to studies of the species composition of plant associations (Ricklefs 1979: 870).

Flyway: a broad-front band or pathway used in migration (Welty 1975:471).

Food chain: a feeding sequence, such as seed-to-songbird-to-raptor, used to describe the flow of energy and materials in an ecosystem (adapted from Ehrlich and Roughgarden 1987:620).

Food web: an abstract representation of the various paths of energy and material flow through populations in the community (Ricklefs 1979:870).

Forest fragmentation: patchwork conversion and development of forest sites (usually the most accessible or most productive ones) that leave the remaining forest in stands of varying sizes and degrees of isolation (Harris 1984:4).

Forest-interior species: species that tend to avoid edge habitats and that require large tracts of forest habitat for nesting and foraging (Whitcomb et al. 1981:139).

Fractal dimension: an index of the complexity of spatial patterns (Turner 1989:175).

Fractal geometry: a method to study shapes that are self-similar over many scales (Turner 1989:175).

Frequency: the number of plots, stations, counts (visits), or intervals in which a species is detected; when expressed as a fraction of the total sampled, it becomes relative frequency (Ralph 1981:578) (cf Density).

Functional response: the change in an individual predator's rate of exploitation of prey as a result of a change in prey density (Ricklefs 1979:870) (cf Numerical response).

Gap analysis: the process of identifying and classifying components of biodiversity to determine which components already occur on protected areas and, conversely, which are un- or underrepresented on protected areas (Scott et al. 1993).

Gap formation: the creation of a habitat patch of different characteristics within a larger patch (Wiens 1989b:201).

Gene flow: the exchange of genetic traits between populations by movement of individuals, gametes, or spores (Ricklefs 1979:870).

Generalist: a species with broad food preferences, habitat preferences, or both (Ricklefs 1979:871) (see Specialist).

Generation time: the average age at which a female produces her offspring, or the average time for a population to increase by a factor equal to the net reproductive rate (Ricklefs 1979:871).

Genetic drift: the change in allele frequency due to random variations in fecundity and mortality in a population (Ricklefs 1979:871).

Genome: a full set of chromosomes (Brown and Gibson 1983:563).

Genotype: the total genetic message found in a cell or an individual (Brown and Gibson 1983:563).

Geographic information system (GIS): a set of computer hardware and software for analyzing and displaying spatially referenced features (i.e., points, lines, and polygons) with non-geographic attributes such as species and age (Johnson 1990:31).

Global change: the large-scale alterations in climate, patterns of land and water use, environmental chemistry, etc., especially alterations related to human activities (Lubchenco et al. 1991).

Guild: two or more co-occurring species' populations that exploit the same type of resources in similar ways. Competition is expected to be especially important within guilds (Wiens 1989a:156–159; Simberloff and Dayan 1991:115).

Habitat: the place where an animal or plant usually lives, often characterized by a dominant plant form or physical characteristic (Ricklefs 1979:871).

Habitat fragmentation: the alteration of a large habitat patch to create isolated or tenuously connected patches of the original habitat that are interspersed with an extensive mosaic of other habitat types (Wiens 1989b:201).

Habitat patches: areas distinguished from their surroundings by environmental discontinuities. Patches are organism-defined (i.e., the edges or discontinuities have biological significance to an organism) (adapted from Wiens 1976:83).

Habitat selection: preference for certain habitats (Ricklefs 1979:871).

Hatching success: percentage of eggs that hatch (Robinson and Rotenberry 1991:280) (syn. hatching rate [Mayfield 1975:459]).

Hatching-year (HY) bird: (1) a bird capable of sustained flight and known to have hatched during the calendar year in which it was banded (or seen) (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1991:5–47); (2) a bird in first basic plumage in its first calendar year (Pyle et al. 1987:26–27).

Heterogeneity: the variety of qualities found in an environment (habitat patches) or a population (genotypic variation) (Ricklefs 1979:872).

Home range: an area, from which intruders may or may not be excluded, to which an individual restricts most of its usual activities (Ricklefs 1979:872) (cf Territory).

Index: (1) the proportional relation of counts of objects or signs associated with a given species to counts of that species on a given area; (2) counts of individuals (e.g., at a feeding station) reflecting changes in relative abundance on a specified or local area (Ralph 1981: 578).

Index method: a counting method involving sampling that yields measures of relative abundance rather than density values (Ralph 1981:578).

Indirect competition: the exploitation of a resource by one individual that reduces the availability of that resource to others (Ricklefs 1979:872).

Indirect effect: (1) the impact on a species caused by affecting the species' competitors, predators, or mutualists (Dunning et al. 1992:173); (2) the impact of toxic chemicals on a species by directly affecting interactions between species. Examples are disruptions in food resources or habitat changes that affect competitive interactions, biomagnification up the food chain, and impacts on populations parasites, symbionts, pollinators, etc. (Harwell and Harwell 1989:521).

Interference competition: competition in which one species prevents the other from having access to a limiting resource (Ehrlich and Roughgarden 1987:624) (cf Exploitation competition).

Interspecific competition: competition between individuals of different species (Ricklefs 1979:873).

Intraspecific competition: competition between individuals of the same species (Ricklefs 1979:873).

Introduced species: species present in an area due to deliberate release by humans (including reintroductions, transplants, and restocked species) or due to accidental release through escape or indirect assistance (adapted from Long 1981:7) (syn. exotic species).

Key factor analysis: a statistical treatment of population data designed to identify factors most responsible for change in population size (Ricklefs 1979:873).

Keystone species: a species whose abundance dramatically alters the structure and dynamics of ecological systems (Brown and Heske 1990:1705).

Landscape: the landforms of a region in the aggregate; the land surface and its associated habitats at scales of hectares to many square kilometers (for most vertebrates); a spatially heterogeneous area (Turner 1989:173); mosaic of habitat types occupying a spatial scale intermediate between an organism's normal home-range size and its regional distribution (Dunning et al. 1992:169).

Landscape change: alteration in the structure and function of the ecological mosaic of a landscape through time (Turner 1989:173).

Landscape complementation: changes in population caused by the relative distributions of habitat patches containing nonsubstitutable resources in a landscape. Example: increased populations in a portion of a landscape where foraging patches and roosting patches are adjacent, compared with parts of the landscape where these patches are isolated (Dunning et al. 1992:170–171) (see Landscape supplementation).

Landscape composition: the relative amounts of habitat types contained within a landscape (Dunning et al. 1992:170).

Landscape ecology: field of study that considers the development and dynamics of spatial heterogeneity, interactions and exchanges across heterogeneous landscapes, the influences of spatial heterogeneity on biotic and abiotic processes, and the management of spatial heterogeneity (Turner 1989:172).

Landscape function: the interactions among the spatial elements, that is, the flow of energy, materials, and organisms among the component ecosystems (Turner 1989:173).

Landscape indexes: indexes of landscape structure (pattern), including richness, evenness, patchiness, diversity, dominance, contagion, edges, fractal dimension, nearest neighbor probability, and the size and distribution of patches (Turner 1989:177–178).

Landscape physiognomy: features associated with the physical layout of elements within a landscape (Dunning et al. 1992:170).

Landscape structure: spatial relationships between distinctive ecosystems, that is, the distribution of energy, materials, and species in relation to the sizes, shapes, numbers, kinds, and configurations of components (Turner 1989:173); composition and extent of different habitat types (landscape composition) and their spatial arrangement (landscape physiognomy) in a landscape (Dunning et al. 1992:170).

Landscape supplementation: changes in populations caused by the distribution of habitat patches containing substitutable resources in a landscape. Example: increased population in a small patch found in a portion of the landscape where residents can easily forage in other nearby similar patches (Dunning et al. 1992:171–172) (see Landscape complementation).

Life form: characteristic structure of a plant or animal (Ricklefs 1979:873).

Life history: a system of interrelated adaptive traits forming a set of reproductive tactics (Stearns 1976:19).

Life table: a summary by age of the survivorship and fecundity in a population, usually of females (Ricklefs 1979:873).

Life zone: a more or less distinct belt of vegetation occurring within, and characteristic of, a particular range of latitude or elevation (Ricklefs 1979:873).

Limiting resource: a resource that is in short supply compared with the demand for it (Ehrlich and Roughgarden 1987:625).

Line transect: a sampling route, through a surveyed area, that is followed by an observer counting contacts over a measured distance (Ralph 1981:578).

Local extinction: disappearance of a population from a habitat patch or local area. Local extinctions can accumulate into regional extinctions and finally global extinction (adapted from Merriam and Wegner 1992).

Logistic equation: mathematical expression for a particular sigmoid growth curve in which the percent rate of increase decreases in linear fashion as population size increases (Ricklefs 1979:874).

Mapping method: see Spot-mapping method.

MAPS: Monitoring Avian Productivity and Survivorship program, which utilizes constant-effort mist netting and banding and intensive point counts during the breeding season at a continent-wide network of stations. MAPS is coordinated by The Institute for Bird Populations (DeSante 1992).

Mayfield method: a method used to calculate the rate of nesting success based on the number of days that a nest was under observation (i.e., nest days of "exposure"); developed by Mayfield (1975).

Measurement bias: a systematic under- or overestimation of the true values due to a difference between the actual measurement and what one intends to measure (adapted from Gilbert 1987:11) (cf Statistical bias).

Measurement endpoint: see Endpoint.

Mesic: moderately moist (Krebs 1985:724).

Metapopulation: a collection or set of local populations living where discrete patches of the area are habitable and the intervening regions are not (Gilpin 1987:127); basic demographic unit composed of a set of populations in different habitat patches linked by movement of individuals (Merriam and Wegner 1992:151).

Microhabitat: the particular parts of a habitat that an individual encounters in the course of its activities (Ricklefs 1979:874).

Migration: regular, extensive, seasonal movements of birds between their breeding regions and their "wintering" regions (Welty 1975:463).

Altitudinal migration—a vertical pattern of migration in which populations that breed in the alpine or subalpine zones in summer move to lower levels in winter (Welty 1975: 475). Inverted altitudinal migration refers to organisms that move to higher levels in winter.

Leap-frog migration—a pattern of migration taken when subspecies of the same species occupy two or more breeding areas (and also wintering areas) in the axis of migratory flight. Subspecies that breed progressively closer to one end of the axis winter progressively closer to the other end. An example is the Fox Sparrow, of which six subspecies inhabit the Pacific coast of North America. On its migration south, each subspecies flies over winter areas already occupied by the subspecies that breeds south of it (Welty 1975:472).

Long-distance migration—a pattern of latitudinal migration used by a species that moves from arctic or temperate regions where it breeds to tropical or subtropical regions for the winter (Welty 1975:465).

Loop migration—a circular pattern of migration such that the migration pathway in the fall differs from the migration pathway in the spring (Welty 1975:472).

Short-distance migration—a pattern of latitudinal migration used by species that move within, rather than between, temperate or tropical zones (Welty 1975:465).

Minimum viable population: a threshold number of individuals that will ensure (with some probability level) that a population will persist in a viable state for a given interval of time (adapted from Gilpin and Soulé 1986:19).

Monitoring: measuring population trends using any of various counting methods (Ralph et al., in press).

Monitoring Avian Productivity and Survivorship program. See MAPS.

Morph: a specific form, shape, or structure (Ricklefs 1979:874).

Mortality: ratio of the number of deaths of individuals to the population, often described as a function of age; death rate (Ricklefs 1979:874).

Multi-brooded: producing more than one clutch or brood per season (Ricklefs 1972:401), usually in reference to a life history trait of a species.

Natal dispersal: movement from birth (natal) site to first breeding or potential breeding site (Greenwood 1980:1141).

Neighborhood effect: increased impact of landscape features located in the immediate neighborhood of a focal patch compared with features farther from the local patch (Dunning et al. 1992:173).

Neotropical migrant: a migratory bird in the Neotropical faunal region. The Neotropical Migratory Bird Conservation Program focuses primarily on species that nest in the Nearctic faunal region and winter in the Neotropical region (Stangel 1992).

Nest parasitism: (1) expression used by some authors (e.g., Thomson 1964:594, Monroe 1991:225) for brood parasitism; (2) taking over nests of other species (Lanyon 1992:78).

Nest success: survival of eggs or nestlings (usually excluding those of brood parasites) (Mayfield 1975:459) (see Hatching success).

Net reproductive rate: the number of offspring that females are expected to bear on average during their lifetimes (Ricklefs 1979:875).

Niche: multidimensional utilization distribution, giving a population's use of resources ordered along resource axes (Schoener 1989:79).

Numerical response: change in the population size of a predatory species as a result of a change in the density of its prey (Ricklefs 1979:876) (cf Functional response).

Parameter: (1) A statistical parameter is a numerical characteristic about the population of interest (Freedman et al. 1978:301); (2) A model parameter is a numerical quantity that mediates the relationships between variables in a model (Starfield and Bleloch 1986:4).

Partners in Flight: a Western Hemisphere program designed to conserve neotropical migratory birds and officially endorsed by numerous federal and state agencies and nongovernment organization (National Fish and Wildlife Foundation 1992:1). Also known as Neotropical Migratory Bird Conservation Program.

Patch dynamics: the change in the distribution of habitat patches in a landscape generated by patterns of disturbance and subsequent patterns of vegetative succession (Pickett and Thompson 1978:29).

Pattern: a statement about relationships among several observations of nature. It connotes a particular configuration of properties of the system under investigation (Wiens 1989a: 18).

Perennial: referring to an organism that lives for more than one year (Ricklefs 1979:876).

Phenotype: the way in which the genetic message of an individual is expressed in its morphology, physiology, and behavior (Brown and Gibson 1983:567).

Phylogenetic species concept: the idea that a species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent (McKitrick and Zink 1988:2) (cf Biological species concept).

Physiognomy: the topography and other physical characteristics of a landform and its vegetation (Brown and Gibson 1983:568).

Point count method: count of contacts recorded by an observer from a fixed observation point and over a specified time interval: fixed distance (radius) point count is limited to individuals within a single fixed distance; variable distance (radius) point count is limited to individuals within distances varying according to species-characteristic detection distances (syn. variable circular plot); and unlimited distance point count includes all individuals without limits, that is, all detections recorded regardless of distance (e.g. the "Indices Ponctuels d'Abondance" [IPA] developed in France) (Ralph 1981:578) (syn. station count method).

Point transect: a transect along which the point count method is used. No recordings are

made between stations (as opposed to strip transects with continuous recordings) (Ralph 1981:578).

Polymorphism: occurrence of more than one distinct form of individuals in a population (Ricklefs 1979:877).

Population: a group of coexisting (conspecific) individuals that interbreed if they are sexually reproductive (Sinclair 1989).

Population viability analysis (PVA): analysis that estimates minimum viable populations (Gilpin and Soulé 1986:19) (syn. population vulnerability analysis).

Postfledging mortality: the death rate of young after fledging, calculated from the following: the fates of young birds after fledging (or hatching in the case of precocial young), when these fates can be observed directly; changes in the ratio between juvenile and adult birds in populations; and the number of surviving young needed to replace adult losses, when adult mortality rates and the production of fledglings are known (Ricklefs 1972:373).

Precision: a quality, associated with a class of measurements, that refers to the way in which repeated observations conform to themselves (Marriott 1990:159).

Primary succession: the sequence of communities developing in a newly exposed site devoid of life (Ricklefs 1979:877).

Process: the operation of some factor or factors that produce a particular relationship among observations (Wiens 1989a:19).

Productivity: the number of young produced per pair of birds, or the reproductive performance of the population, estimated as the proportion of young in the total population just after the breeding season (Ricklefs 1972:417).

Proximate factors: aspects of the environment that organisms use as cues for behavior; for example, daylength (Ricklefs 1979:877) (cf Ultimate factors).

Quadrat: a small sample plot, usually square or rectangular (Ralph 1981:578).

Rate of increase: a measurement of the change in numbers of a population. The finite, or geometric, rate of increase (λ) is the factor by which the size of a population changes over a specified period (Caughley 1977:51; Ricklefs 1979:871). The exponential rate (r) is the power to which e (the base of natural logarithms) is raised such that $e^r = \lambda$ (Caughley 1977:52). Caughley (1977:109) distinguished the following exponential rates:

ρ—the intrinsic rate of increase in the best of all possible environments.

Intrinsic rate of increase—the rate at which a population with a stable age distribution grows in a given environment when no resource is in short supply (syn. Malthusian parameter [Ricklefs 1979:874]).

Observed rate of increase—the rate of increase at which a population increases over time.

Potential rate of increase—the rate that would result if the effect of a given agent of mortality were eliminated.

Survival-fecundity rate of increase—the exponential rate at which a population would increase if it had a stable age distribution appropriate to its current schedules of age-specific survival and fecundity.

Ricklefs (1979:873) defined the innate capacity for increase as the intrinsic growth rate of a population under ideal conditions without the restraining effects of competition.

Recovery plan: a plan that details actions or conditions necessary to promote species recovery, that is, improvement in the status of species listed under the Endangered Species Act to the point at which listing is no longer appropriate. Plans are required for virtually all listed species (adapted from Rohlf 1989:87–89).

Recovery team: a group, established by the U.S. Fish and Wildlife Service (USFWS) or National Marine Fisheries Service (NMFS) (the agencies that share authority for listing species as endangered or threatened under the Endangered Species Act), that prepares a recovery plan for a species listed under the Endangered Species Act. The team usually

consists of representatives from agencies that are charged with implementing the plan, scientists with expertise about the species involved, representatives from industries that may be affected by the plan, and USFWS/NMFS personnel (adapted from Rohlf 1989: 88–89).

Recruitment: the addition of new individuals to a population by reproduction (Ricklefs 1979:878), commonly measured as the proportion of young in the population just before the breeding season (Ricklefs 1972:418).

Refugium: an area that remains unchanged while areas surrounding it change markedly; hence the area serves as a refuge for species requiring specific habitats (Brown and Gibson 1983:569).

Relative abundance: a percent measure or index of abundances of individuals of all species in a community (Ralph 1981:578) (syn. dominance [in Europe]; cf Index, Frequency, Density).

Relative frequency: see Frequency.

Remote sensing: the imaging of earth features from suborbital and orbital altitudes, using various wavelengths of the visible and invisible spectrum (Richason 1978:xi).

Resident: inhabiting a given locality throughout the year; sedentary (Welty 1975:463).

Resource: a substance or object required by an organism for normal maintenance, growth, and reproduction (Ricklefs 1979:878).

Restoration ecology: the re-creation of a natural or self-sustaining community or ecosystem (Jordan et al. 1987:331).

Riparian: along the bank of a river or lake (Ricklefs 1979:878).

Secondary succession: progression of communities in habitats where the climax community has been disturbed or removed entirely (Ricklefs 1979:878).

Second-year (SY) bird: a bird in its second calendar year of life (Pyle et al. 1987:27; Canadian Wildlife Service and U.S. Fish and Wildlife Service 1991:5–47).

Sedentary: not migratory; see also Resident (Welty 1975:46).

Sere: a series of stages of community change in a particular area leading toward a stable state (Ricklefs 1979:879).

Sink habitat: a habitat in which reproduction is insufficient to balance local mortality. The population can persist in the habitat only by being a net importer of individuals (adapted from Pulliam 1988:653–654).

Sink population: a population that occupies habitat types in which reproductive output is inadequate to maintain local population levels. The population may be replenished by emigrants from source populations (Wiens and Rotenberry 1981:531).

Source habitat: a habitat that is a net exporter of individuals (Pulliam 1988:654).

Source population: a population that occupies habitat suitable for reproduction, in which the output of offspring results in a population that exceeds the carrying capacity of the local habitat, promoting dispersal (adapted from Wiens and Rotenberry 1981:531).

Specialist: a species with narrow food preferences, habitat preferences, or both (after Ricklefs 1979:871) (see Generalist).

Species: a group of actually or potentially interbreeding populations that are reproductively isolated from all other kinds of organisms (Ricklefs 1979:880).

Species-area relationship: a plot (often log-log) of the numbers of species of a particular taxon against area, such as islands or other biogeographic regions (Brown and Gibson 1983:570).

Species diversity: see Diversity.

Species richness: the number of species in a given area (Ralph 1981:578).

Spot-mapping method: a census procedure that plots on a map individuals seen or heard in a surveyed area. The survey is usually conducted over a period of days or weeks in a

season, and individual territories or home ranges are then demarcated by examining the clusters of observations. Used in Breeding Bird Census (Ralph 1981:578) (syn. Territory-mapping).

Stable age distribution: the proportions of the population in different age classes when the rate of increase has converged to a constant (which depends on the fixed schedules of survival and fecundity). The ratios between the numbers in the age classes are constants (Caughley 1977:89).

Station: (1) the area within which observations made from a point are recorded by the observer (or often synonymous with "point," see Point count method) (Ralph 1981:578); (2) a monitoring station is an area of usually less than about 50 ha where intensive censuses, nest searching, and/or mist netting are conducted (Ralph et al., in press).

Statistical bias: a difference between the expected value of an estimator and the population parameter being estimated (Gilbert 1987:12) (cf Measurement bias).

Stenotopic: found in only one or a relatively small number of habitats (MacArthur and Wilson 1967:191).

Stressor: any chemical, physical, or biological entity that can induce adverse effects on individuals, populations, communities, or ecosystems (Risk Assessment Forum 1992:1).

Strip transect method: a procedure using a strip of land, or water, of fixed direction that is sampled visually and/or aurally by an observer. Counts may be one of the following: fixed distance (width) counts limited to a strip of set width for all or specially chosen species; variable distance (width) counts, with different, species-specific widths that are determined to reflect detection attenuation; or unlimited distance counts, in which all detections are recorded regardless of distance (Ralph 1981:578) (syn. belt-transect).

Stochastic: implies the presence of a random variable (Marriott 1990:197).

Subclimax: a stage of succession along a sere prevented from progressing to the climatic climax (i.e., the steady-state community characteristic of a particular climate) by fire, grazing, and similar factors (Ricklefs 1979:880).

Subspecies: subpopulations within a species that are distinguishable by morphological characteristics and, sometimes, by physiological or behavioral characteristics (Ricklefs 1979: 880) (syn. race).

Succession: replacement of populations in a habitat through a regular progression to a stable state (climax) (Ricklefs 1979:880).

Survey: an enumeration or index of the number of individuals in an area from which inferences about the population can be made (Ralph 1981:578) (cf Census, Count).

Survival: the proportion of newborn individuals alive at a given age (Ricklefs 1979:880).

Sympatric: occurring in the same place, usually referring to areas of overlap in species distributions (Ricklefs 1979:880).

Syntopic: pertaining to populations or species that occupy the same macrohabitat (Lincoln et al. 1982:242).

Territory: any area defended by one or more individuals against intrusion by others of the same or different species (Ricklefs 1979:881) (cf Home range).

Territory-mapping: see Spot-mapping method.

Third-year (TY) bird: a bird in its third calendar year of life (Pyle et al. 1987:27).

Transect: a cross section of an area along which the observer moves in a given direction (Ralph 1981:578) (see Line transect, Point transect, Strip transect method).

Trophic: pertaining to food or nutrition (Ricklefs 1979:881).

Trophic level: the position in the food chain determined by the number of energy-transfer steps to that level (Ricklefs 1979:881).

Trophic structure: organization of the community based on feeding relationships of populations (Ricklefs 1979:881).

Turnover: the process of local extinction (e.g., on islands) of some species and their replacement by other species. The turnover rate is the number of species eliminated and replaced per unit time (MacArthur and Wilson 1967:191).

Ultimate factors: aspects of the environment that are directly important to the well-being of an organism (for example, food) (Ricklefs 1979:881). Ultimate factors are concerned with fitness (Lack 1954:5) (cf Proximate factors).

Variable circular plot: see Point count method.

Variable-distance method: see Strip transect method, Point count method.

Variance: a statistical measure of the dispersion of a set of values about its mean (Ricklefs 1979:881).

Winter Bird Population Study (U.S.): a program of the National Audubon Society involving census of wintering birds by counting and mapping, but not depending on persisting occupation of territories or home ranges (Ralph 1981:578) (cf Breeding Bird Census).

Xeric: referring to habitats in which plant production is limited by lack of water (Ricklefs 1979:882).

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SHORT COMMUNICATIONS

Spring and fall migration of Peregrine Falcons from Padre Island, Texas.—Currently, little data exist on the behavior of migrating Peregrine Falcons (*Falco peregrinus*). Enroute ecology of migrant peregrines has been studied at stopover areas such as Asseategue Island, Maryland (Ward and Berry 1972, Ward et al. 1988) and Padre Island, Texas (Enderson 1965, Hunt et al. 1975, Hunt and Ward 1988). Information on migratory behavior of peregrines has been obtained indirectly during short periods of observation and by band recovery data (Enderson 1965, Kuyt 1967, Shor 1970, Henny and Clark 1982, Yates et al. 1988, Schmutz et al. 1991). For example, estimates of speed for migrating raptors have been obtained either by timing migrants over short distances (Broun and Goodwin 1943, Kerlinger 1989) or by calculating the average speed required for migrants to have travelled a given distance, usually during several days and hundreds or thousands of kilometers (e.g., Layne 1982, Foy 1983, Heintzelman 1986).

In this study, we report the pathways and migratory behavior of one fall southbound and one spring northbound migrating Peregrine Falcon, tracked with radiotelemetry after their departures from Padre Island, Texas. Daily flight times, daily distance travelled, and speeds of the spring and fall migrating Peregrine Falcons are presented and compared. Arrival times at, and departure from, night roosts are presented along with observations of flight behavior while on migration.

Study area and methods.—Padre Island, Texas, is a barrier island extending approximately 220 km from Corpus Christi southward to the mouth of the Rio Grande. Padre Island as stopover habitat for migrant peregrines has been described previously by Hunt et al. (1975) and Hunt and Ward (1988) and is well known for large concentrations of both fall and spring migrating peregrines (Hunt et al. 1975).

Between 10 April and 26 May 1985, approximately 200 peregrines were captured, banded, and released as part of ongoing banding studies by Kenton Riddle and coworkers. Four females were radio-tagged 21–27 April. Between 14 and 18 October, three females were radio-tagged and released at Padre Island. Captured falcons were banded with U.S. Fish and Wildlife Service aluminum leg bands and fitted with Telonics model 040 transmitters. The radios were attached to the underside of the two central rectrices with linen thread and cyanoacetate glue. Transmitter antennas were attached to the rachis of one of the central rectrices and extended approximately 10 cm beyond the tip of the tail. A Telonics TR-2 receiver and TS-1 scanner were used to track the migrating peregrines. Two side pointing "H" type receiver antennas were attached to the wingstruts of a Cessna 172 aircraft used for tracking the migrating falcons. All radiotagged falcons were monitored between four and eight times per day from the air to determine initiation of migration. Due to the difficulties encountered while tracking migrating raptors, only a single peregrine was monitored each season on its migration flight from Padre Island. The first radio-tagged Peregrine Falcon to leave during each season was monitored. During migration, the peregrines were monitored nearly continuously throughout the day from early morning to the time they roosted in the afternoon. Monitoring was mostly from the air, but on several occasions, the falcons were monitored while the plane was on the ground.

Once in migration, the falcons' daily flight distance (DFD), daily flight time (DFT), and ground speeds were calculated and recorded. Daily flight distance was the total ground distance covered by a falcon from departure roost to evening roost. Daily flight time was the total time the falcon was in flight. Because the falcons sometimes had departed by the time we reached the previous night's roost site, it was necessary to estimate time of departure.

Estimated time of departure (ETD) was extrapolated from the speed and distance of the falcon from the roost when first encountered on its morning flight. Because the falcons were usually intercepted a short distance from the roost site, ETD is believed to be close to actual time of departure. Hereafter, ETD will be used to refer to both estimated and actual time of departure. Estimated time of roosting (ETR) is the time the falcons stopped flying and perched to roost in the afternoon.

Ground speeds (cross country speeds) were estimated in km/h by determining the distance and time elapsed between two location points. The number of precise locations varied daily because of the logistical difficulties of tracking migrating raptors with aircraft. The main problem was finding a place to refuel along the route of the migrating falcon, which on several occasions, caused us to interrupt monitoring and deviate from the falcon's route.

Wind direction and speed during the monitoring of migrating falcons, as well as significant changes such as fronts were noted. Daily wind speeds were classified into one of three categories, light (<10 km/h), moderate (10–19 km/h), and strong (>19 km/h).

Daily flight time, daily distance, and speeds of the two falcons were compared using Mann-Whitney *U*-tests (Conover 1980). It is possible that measurements obtained from a single falcon while on migration may violate the assumption of independance of data points; however, Mann-Whitney *U*-test is recommended by Kenward (1987) for similar analyses.

Results.—During the spring migration, four falcons were monitored on Padre Island and moved up to 70 km/day on the island, but they usually returned to a roosting site near that of the night before. During the fall southward migration, the falcons (three) moved less than 10 km from the point of capture, generally in a north-south direction. The movements of spring and fall migrant falcons, while on Padre Island, are for hunting and foraging (Hunt et al. 1975).

The spring migrant, an adult female, was tracked a total of four days from the time she left Padre Island (3 May), covering 2732 km in 46.8 h of effective flight time. The fall migrating peregrine, an immature female, was tracked seven days and flew 1803 km in 37.8 h of effective flight time. On the first day of migration, 3 May, the spring migrant flew northwest and the ETD was 10:30. In the fall, the first peregrine to leave the island flew southwest on 18 October, two days after being radiotagged. The ETD (10:45) for the fall peregrine was similar to the spring migrant's ETD. The first day of migration, the fall migrating peregrine travelled a total of 105 km in 4.8 h, while the spring migrant flew 414 km in 8.5 h.

The direction of flight was constant for the spring migrant but varied for the fall migrating peregrine (Fig. 1). During the spring migration, the falcon maintained a true track of 346°, plus or minus 5°, from Padre Island to the last point of observation in Saskatchewan, approximately 20 km north of the U.S.-Canada border. It crossed the states of Texas, Oklahoma, Colorado, Wyoming, and Montana, parallel to the eastern Rocky Mountains.

The fall migrating peregrine began flying southwest, then continued south and finally east at the Isthmus of Tehuantepec (Fig. 1). The route paralleled the Gulf of Mexico coast through the Mexican states of Tamaulipas and Veracruz to the Isthmus of Tehuantepec. Beyond the Isthmus, the peregrine abandoned the coast and flew directly east along a route that took it through Tabasco and Chiapas in Mexico, over northern Guatemala, and into Belize until it reached the Belize coast. From the Belize coast, it flew eastward into the Carribean ocean where tracking was terminated.

The spring migrant on several occasions left the roost site before sunrise, while the fall peregrine always commenced flight after sunrise (Table 1). Missing information from the second day was due to our need to clear customs and immigration with the Mexican authorities.

DFDs of the north and south migrating peregrines differed significantly ($U = 34$, $P <$

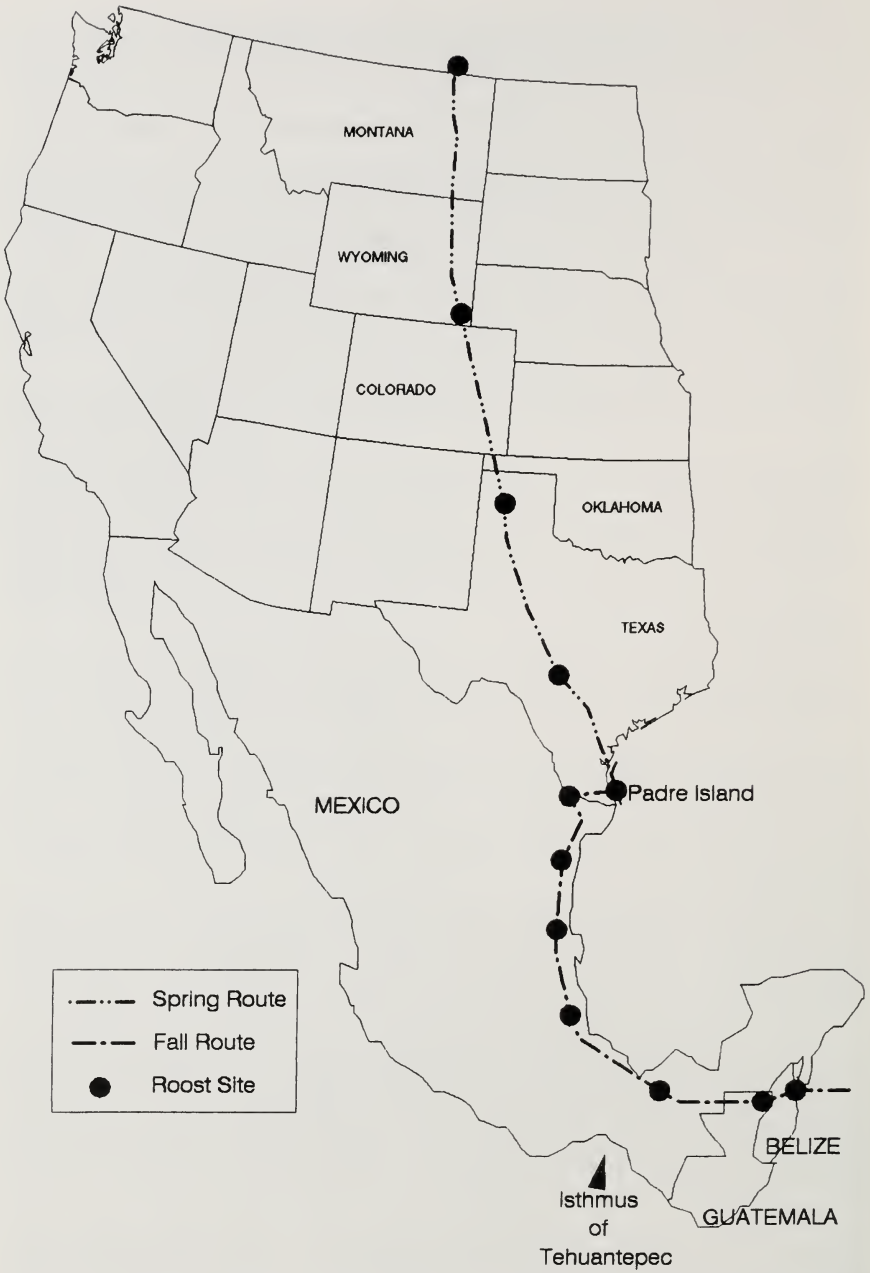

FIG. 1. Migratory routes of one spring and one fall migrating Peregrine Falcon from South Padre Island, Texas.

TABLE 1
ESTIMATED TIME OF DEPARTURE AND ROOSTING TIMES FOR SPRING AND FALL MIGRANT PEREGRINE FALCONS RELATIVE TO SUNRISE AND SUNSET

Day of migration	ETD	Relative to Sunrise	ETR	Relative to sunset
		Spring migrant		
1	10:30	—	18:00	+41
2	05:00	+28	18:46	+106
3	04:50	+15	14:00	—
4	05:00	−14	19:28	+18
		Fall migrant		
1	10:45	—	—	—
2	—	—	17:06	+31
3	11:15	—	16:10	+82
4	07:00	−53	17:20	+13
5	07:00	−55	17:00	+35
6	07:00	−56	16:05	+96
7	07:30	−86	10:30	—

(+) Minutes before sunrise or sunset.
(−) Minutes after sunrise or sunset.

0.025) (Fig. 2). The north migrating falcon averaged 708 km of DFD (SD = 223.5, range 414–915), while the south migrating peregrine averaged 257 km (SD = 140, range 105–460). Both spring and fall migrants showed a gradual increase in DFD as the migration progressed, with the exception of the seventh day of the fall migrant, when it reached the Belize coast.

The DFTs of the two falcons differed significantly ($U = 30$, $P = 0.05$); the spring migrant flew several hours more each day than the fall migrant (Fig. 2). The spring and fall migrants DFTs averaged 12.02 h (SD = 2.7) and 8.75 h (SD = 2.8), respectively. The DFT of the north bound peregrine showed a trend similar to DFD, increasing sequentially each day. The southward migrating peregrine did not show a similar trend, the DFT remained more constant with exceptions on the third and last day of monitoring. On the last day of migration the falcon reached the Belize coast in only 3.5 h of flying, after which no movements were observed until the following day.

Ground speeds calculated for the two falcons were significantly different ($U = 258$, $P < 0.001$). The spring and fall migrant mean speeds were 58.1 km/h (SD = 13.1, range 38–90, N = 17) and 33.6 km/h (SD = 9.6, range 17–52, N = 13), respectively. Only small variations in speeds on a given day were observed for the fall migrating peregrine. These variations were usually less than 8 km/h, with one exception. The speeds calculated on the same day for the spring migrant ranged from a minimum of 12 to a maximum of 40 km/h.

Wind velocities during the spring tracking were always moderate and from a southeast direction, with a single exception. On the second day of migration (5 May), a strong cold front moved from the northwest. During the fall tracking wind velocities varied from calm to light and wind direction was varied, being from the southeast (days 1, 2, 3, and 6 of migration), west (day 7), and northeast (days 4 and 5).

Discussion.—The north-south movements of radiotagged falcons in this study contrast

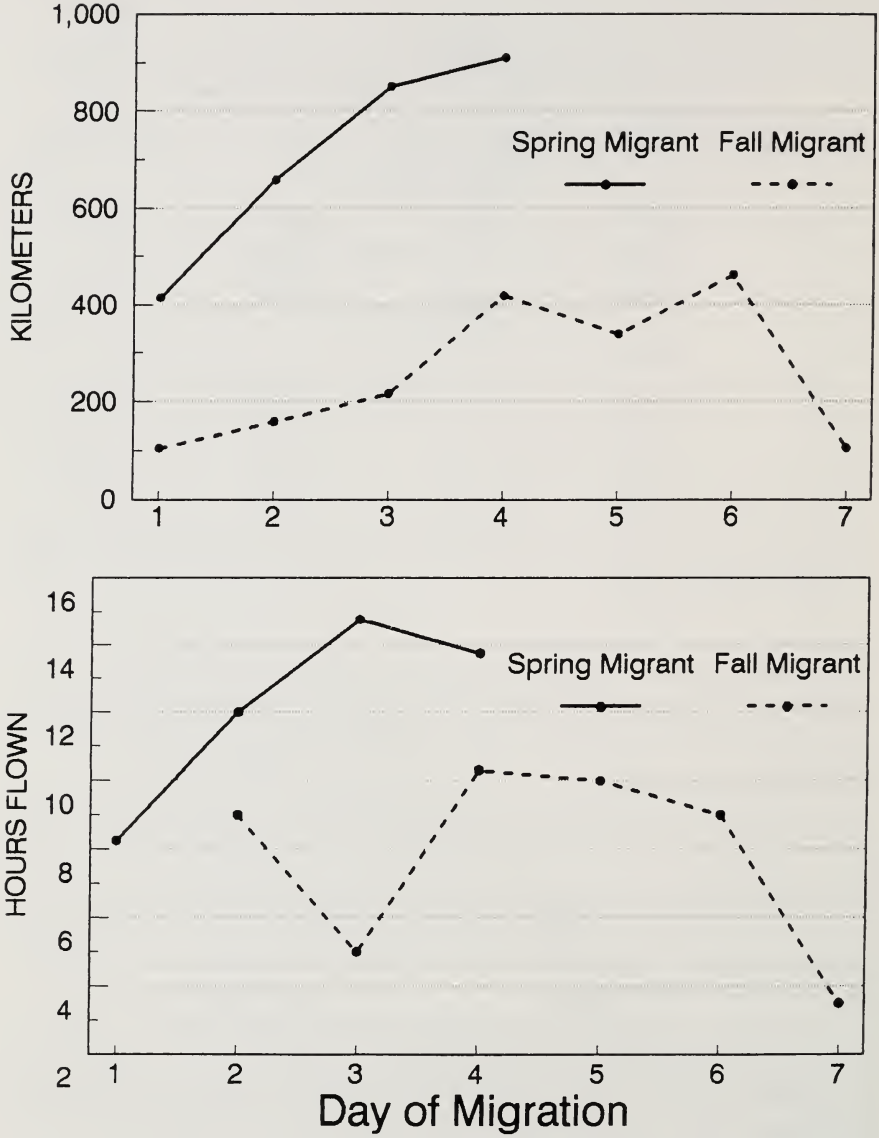

FIG. 2. Daily flight distance and daily flight time of one spring and one fall migrating Peregrine Falcon.

with those observed by Enderson (1965) who found no evidence of north-south movements nor any alternative directional movements of peregrines on Padre Island. The movement of Peregrine Falcons we observed lengthwise along Padre Island, clearly supports the notion (Enderson 1965, Hunt et al. 1975, Hunt and Ward 1988) that this is a very important stopover site for both spring and fall migrating peregrines.

Conflicting accounts exist regarding the type of migratory flight used by Peregrine Falcons. Heintzelman (1986) reports that this species does relatively little thermal soaring, while Cochran (1975) suggests that peregrines use circle (thermal) soaring to a great extent. We believe peregrines used both types of flight while migrating. Using speed to indicate flight type, the speed at which the spring migrant flew in most cases excludes the possibility of thermal soaring. Reported long distance thermal soaring and gliding speeds estimated for raptors do not exceed 50 km/h (Hopkins 1975, Harmata et al. 1985, Smith 1985, Smith et al. 1986, Leshems 1987, others in Kerlinger 1989 pp. 283–286) while this falcon consistently flew at speeds greater than 50 km/h. Only five of 17 speed estimates were less than 50 km/h. It is likely the fall migrant used thermal soaring and gliding more extensively, since its calculated speeds were less than 50 km/h, with a single exception. Thermal formation is not well developed until 3–5 h after sunrise and continues until the sun ceases to heat the earth's surface (Kerlinger 1989). The late departure times and the slow progress observed during at least three mornings by the fall peregrine may indicate that it was waiting for thermal formation to begin flying. However, it is also possible that it may have been hunting.

The great differences observed in speeds and DFD between the two falcons may be due to the age or experience of the falcons, since the spring peregrine was an adult female while the fall migrant was an immature female. While migratory behavior (migratory orientation, feeding, resting) and most aspects of avian migration are believed to be under endogenous or genetic control (Berthold 1990, Gwinner 1990), experience is likely to be important in fine tuning certain aspects of migration. For example, specific migratory pathways and location of stopover areas may be easier to find and use once the route has been travelled previously.

The daily flight distances observed in the two peregrines studied here are greater than previously reported for peregrines. Cochran (1975) reported an average DFD of 111 mile/day (179 km) for a fall migrating peregrine with the longest distance travelled in one day reported as "about 200 miles" (322 km). The average and maximum DFD travelled by the fall migrant in this study are greater then the peregrine tracked by Cochran. The peregrine tracked by Cochran is reported to have used soaring and gliding flight regularly, and hunted as much as twice a day. During fifteen days of migration, the falcon tracked by Cochran (1975) is said to have hunted daily, usually several times, during morning and afternoons. The behavior (gliding flight and hunting), which contrasts with the behavior of the falcon in this study, would greatly reduce the speed and distance a falcon could travel in one day. Hunting by the fall migrant peregrine during this study is not likely to have occurred in the afternoon, since it flew continuously throughout the day and no movements were observed once roosted in the afternoon. At most, the falcon tracked in this study during fall could have hunted on two occasions during the seven days it was monitored after departure from Padre Island.

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Sex-related local movement in adult Rock Kestrels in the eastern Cape Province, South Africa.—Long-distance migration in the Rock Kestrel (*Falco tinnunculus rupicolus*) has not been recorded in southern Africa (Moreau 1972), although it is a well-known phenomenon for its European conspecific the Common Kestrel (*F. t. tinnunculus*) (Village 1990). Of 776 Rock Kestrels ringed in southern Africa, nine birds have been recovered, of which only one was found farther than 30 km from where it was ringed (SAFRING, pers. comm.). Partial local movement of Rock Kestrels in South Africa, especially altitudinal movements, have been reported by several authors (Rowan 1964, Tarboton and Allan 1984, Hockey et al. 1989). It remains unclear, however, whether these movements are sex- or age-related, whether the kestrels return to the same area, and how long they are absent from their breeding sites.

Study area and methods.—Rock Kestrels are found throughout southern Africa but are most common in the drier mountainous regions. They feed mostly on invertebrates, reptiles, and small mammals and breed on cliffs or in old nests of Pied and Black crows (*Corvus albus* and *C. capensis,* respectively) in trees from August to February (Steyn 1982). I studied 10 territorial pairs of Rock Kestrels in the foothills of the Winterberg Mountain Range (32°10′S, 26°20′E), Tarkastad District, South Africa from April 1990 to June 1991. The average annual rainfall is 426.4 mm with an average daily maximum temperature of 19.0°C in winter and 29.1°C in summer. Kestrels were caught using a bal-chatri trap (Berger and Mueller 1959) and marked individually with color rings. Each territory was searched for kestrels at least once a week. First- and last-sighting dates were used as a measure of arrival and departure dates.

Results and discussion.—On average, females left their territories before males, were away longer, and returned after males. All the females, except one, and six of the males left their territories for longer than 25 days (N = 10 pairs). Of the five pairs for which the date of departure was known for both individuals, the female always left before the male (Table 1). In these pairs, the male returned before the female in three instances, with one returning at the same time as the female and one after the female. All the kestrels that left their territories during winter returned to the same territories prior to the breeding season. The male that returned after his female, and one other male, lost their territories to males that occupied the territories during their absence. One of these new males paired with the resident female, and the other paired with a new female.

Prey-strike rates have been shown to follow cyclic vole availability in kestrels in the Netherlands (Rijnsdorp et al. 1981). Prey-strike rates during perch hunting, the predominant hunting method in this study, were used as an indication of food availability to individual kestrels (Table 2). Although prey-strike rate can be highly misleading if there are large differences in prey size, arthropods weighing between 0.1 and 3 g comprised 97.9% (N = 1962 prey items) of the diet (Van Zyl, unpubl. data). Prey-strike rates decreased until birds left the area with an increase on their return.

Table 1

Differences in Departure, Absence and Arrival Times of Five Adult Kestrel Pairs for Which Exact Departure and Arrival Dates Were Known

Movement status	Males (SE)	Females (SE)	Paired *t*-value
Departure	29.8 (7.9)	23.2 (6.8)	2.93*
Absence	54.6 (14.4)	90.8 (11.2)	2.78*
Arrival	84.4 (13.3)	114.0 (5.2)	2.03

Departure and arrival dates are in days starting from 1 April, while durations of absence are in days away.
* $P < 0.05$

In this study, the adult kestrel movements can be interpreted as partial local movement, since not all individuals left the study area, and the short period that they were away suggests that they did not move far.

Kestrels that stayed in their territories during the winter were able to retain their territories and hence had a high chance of breeding the following season. The poor food supply during winter suggests that they ran the risk of starvation. Conversely, the kestrels that left the area

Table 2

Individual Strike Rates (Str·h $^{-1}$ Perch Hunting) during Winter 1990 as an Indication of Food Availability to Kestrels

Territory	Sex	May	June	July	August	September	October
Oxford	M	?[a]	2.1	?	?	4.2	Predated
		(0)	(29)	(0)	(0)	(43)	
Oxford	F	2.2	Absent	Absent	Absent	1.2	1.2
		(27)				(167)	(49)
Sumhill	M	?	?	1.4	1.2	5.5	?
		(0)	(0)	(216)	(204)	(66)	(0)
Sumhill	F	?	3.7	2.9	2.3	?	4.6
		(0)	(131)	(333)	(131)	(0)	(26)
Spring	M	2.6	1.7	Absent	1.7	Evicted	
		(70)	(456)		(35)		
Spring	F	2.5	2.0	Absent	1.5	Left area	
		(144)	(182)		(40)		
Fair View	M	1.5	Absent	Absent	Absent	8.3	Evicted
		(111)				(80)	
Fair View	F	?	Absent	Absent	Absent	3.0	4.3
		(0)				(239)	(196)
Lochie	M	?	2.1	3.0	2.9	3.1	3.5
		(0)	(286)	(345)	(389)	(688)	(69)
Lochie	F	3.5	Absent	Absent	2.2	2.1	3.8
		(137)			(440)	(623)	(350)

[a] Question marks indicate months for which no foraging data were available for the specific individual. Observation time spent perch hunting in minutes is given in brackets. The Spring and Fair View male kestrels were evicted by adult male kestrels that had moved into the territories prior to their return.

would have a higher survival but would possibly not have a territory on their return, and would forego a breeding attempt. There is, therefore, a trade-off between the chance to breed and the risk of mortality during winter. I suggest that both male and female kestrels are influenced to leave the area because of a critical food shortage, and that females return once the food supply is adequate. Males are able to leave later because of lower energetic requirements due to their smaller body size (males are 7.3% smaller than females; N = 57; unpubl. data). I suggest that males return early to procure and maintain a territory before the return of the females, even though food availability might still be low. Territorial behaviour was most frequently observed during the early breeding season in kestrels in England (Wiklund and Village 1992). In two instances where males returned to their territories relatively late in the season (August), they both lost their territories to males which had arrived earlier or did not leave. The longer that males were absent from their territories the greater was the chance of losing their territories, especially in the early breeding season when the floater population was at its peak. While males' early return was essential to maintain a territory, females needed only to return once food conditions were adequate. Females paired with the resident males of the territories, and, in one case, a new male. Strike rates of the single female that left her territory after it was taken over by a new male indicate that prey availability was poor. This may have been the reason for her leaving rather than the new male. The fact that the new pair in that territory failed to breed that season, is further evidence of the poor food availability. The small number of floating kestrels suggests that food supply remains the limiting resource throughout the year.

Village (1985) reported a similar movement of kestrels in and out of his Scotland study area. There was, however, an influx of wintering kestrels which was not observed in this study, suggesting that food conditions were too poor to maintain a large winter population. In Scotland, there was a similar bias towards males during winter, with females returning, on average, only four days later than males. Village's observations supported Piechocki's (1982) view that male kestrels settled in a territory first and then attracted a female. In contrast, data from this study support the idea that females return to their breeding sites rather than to prospective males. No females changed territories from 1990 to 1991, nor were they seen in any territory other than their own. Removing males and observing female pairing patterns would test whether females select sites rather than males. Female Merlins *Falco columbarius* have also been reported to return to breeding sites rather than their mates (Warkentin et al. 1991).

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Daily movements of Northern Bobwhite broods in southern Texas.—Understanding the potential mobility of individuals is important when describing the spatial distribution of a species' habitat components. Information concerning the daily movements of Northern Bobwhite (*Colinus virginianus*) broods is lacking, making descriptions of optimum brood habitat difficult. We here present information on daily home ranges and minimum distances traveled of radio-marked Northern Bobwhite broods in southern Texas.

Study area and methods.—We conducted field work from March through August 1989 and 1990 on the Zachry Randado Ranch in Jim Hogg and Zapata counties, Texas. The dominant plant community on the ranch was mesquite (*Prosopis glandulosa*)-mixed brush (Drawe and Higginbotham 1980). Annual precipitation in the area averages 58.2 cm and summer temperatures are high (July mean is 31°C) (N.O.A.A. 1989–1990).

Adult bobwhite were captured with grain sorghum-baited funnel traps (Wilbur 1967) during March and April. Captured females were fitted with backpack-mounted radio transmitters (Marshall and Kupa 1963) weighing either 4.3 or 8.5 g in 1989 and 4.3 g in 1990. Radio-marked females were located 2–6 times/week, and consecutive identical location estimates identified hens that were incubating.

If a radio-marked female hatched at least one egg, we waited until chicks were 3–6 days old before monitoring the brood. Thereafter, we obtained one location series/week for broods until they reached six weeks of age. A location series consisted of five location estimates/day, with one location each during 03:00–06:00, 08:00–09:30, 12:00–14:00, 18:00–20:00, and 22:00–23:00 CST. We estimated brood locations by approaching within approximately 30 m of the radio-marked female and then partially circling its estimated location (White and Garrott 1990:42). Location estimates were plotted on an aerial photograph of the study area (scale 1:4800).

We examined night roost sites to learn if radio-marked females and their chicks became separated. If no chick feces were found at the sites, separation was confirmed by flushing females and directly observing chicks or if hens exhibited brood-tending behavior (short, fluttering flight and excited calling).

Minimum daily distances moved by broods were estimated by adding the distances between the five location estimates in a daily series. Daily home ranges were calculated using the minimum convex polygon method (Hayne 1949) using program HOME RANGE (Samuel et al. 1985). We compared means of movement variables for ≤2-week-old broods (prefledging) with those for ≥three-week-old young (postfledging) using Wilcoxon tests (Zar 1984:139). We used a $P \leq 0.1$ significance level to discern differences between means.

Results.—Sixteen daily location series were analyzed for five broods (1–5 series/brood). Mean home ranges ($P = 0.072$) and distances traveled ($P = 0.020$) differed with brood age. Daily home ranges and minimum distances traveled averaged 0.7 ± 0.4 ha (±SE) and 277 ± 65 m, respectively, for prefledging broods (N = 7). These variables averaged 1.4 ± 0.4 ha (N = 9) and 589 ± 74 m, respectively, for postfledging broods.

Discussion.—Lehmann (1984:106) hypothesized that Northern Bobwhite broods moved "no farther than necessary to find satisfactory accommodations," but did not attempt to quantify movements. Bell et al. (1985) reported daily distances traveled by adult bobwhites in Louisiana averaged 370 m in spring, which is generally less than the broods we studied traveled when they were > one week old. This discrepancy may be because we used five radiolocations for distance estimation rather than the three used by Bell et al. Crim and Seitz (1972) found daily ranges of adult bobwhites of both sexes averaged 1.6 ha, which is approximately equal to our ≥three-week-old daily brood ranges.

The positive association between brood age and movements is similar to that reported for Ring-necked Pheasants (*Phasianus colchicus*) (Warner 1984) and Gray Partridges (*Perdix perdix*) (Church 1980). Warner (1984) also found that pheasant broods moved less in fine-grained than in coarse-grained landscapes. Habitat types (e.g., brush and herbaceous vegetation) on our study area were well interspersed (i.e., distances from any point on our study area to a mature brush-herbaceous vegetation edge were generally <125 m). Thus, if this association is also valid for Northern Bobwhites, we would expect movements of the broods we studied to be small relative to those of broods in areas where habitat types are less interspersed (e.g., cropland).

Our data lacked spatial and, to a lesser extent, temporal replication. Future research on Northern Bobwhites should describe brood movements in other regions and landscape patterns within the species' range.

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Correlation between raptor and songbird numbers at a migratory stopover site.—Certain landscape features, such as coastlines, often concentrate raptors during their migration (Mueller and Berger 1967, Dunne and Clark 1977, Bednarz et al. 1990). A number of falconiform species that cross the Gulf of Mexico during both the spring and fall migrations have been seen on the barrier islands that parallel the northern Gulf of Mexico (Moore et al. 1990). These islands are important stopover areas for migrating songbirds (Moore and Kerlinger 1987) because they represent their first opportunity to rest and replenish depleted fat stores following trans-Gulf flight. The islands may also be important for migrating hawks by virtue of the concentration of songbird migrants (Kerlinger 1989). Passerine migrants are an important resource for raptors during migration, and migrating raptors have been observed hunting at stopover sites (Hunt and Ward 1988, Lindström 1989, Moore et al. 1990).

I examined the co-occurrence of raptors and songbirds during migration by observing the passage and behavior of raptors at a migratory stopover site. The work was conducted on East Ship Island (ESI), a barrier island which lies approximately 19 km from the Mississippi coast (see Kuenzi et al. 1991), between 2 April and 6 May 1991. Although the focus of research on the island was the stopover ecology of songbirds, I and three field assistants noted the presence and behavior of raptors throughout the daylight hours. We identified the species, whether or not it was flying (an indicator of predatory activity), any attacks on migrants, and evidence of feeding on migrants. Some individual raptors may have been counted more than once as the raptors were not marked.

We counted 50 Merlin (*Falco columbarius*) and 55 Peregrine Falcon (*F. peregrinus*) observations. Five American Kestrels (*F. sparverius*) and three Swallow-tailed Kites (*Elanoides forficatus*) were also seen, but their numbers do not permit statistical analysis. Falcon sight-

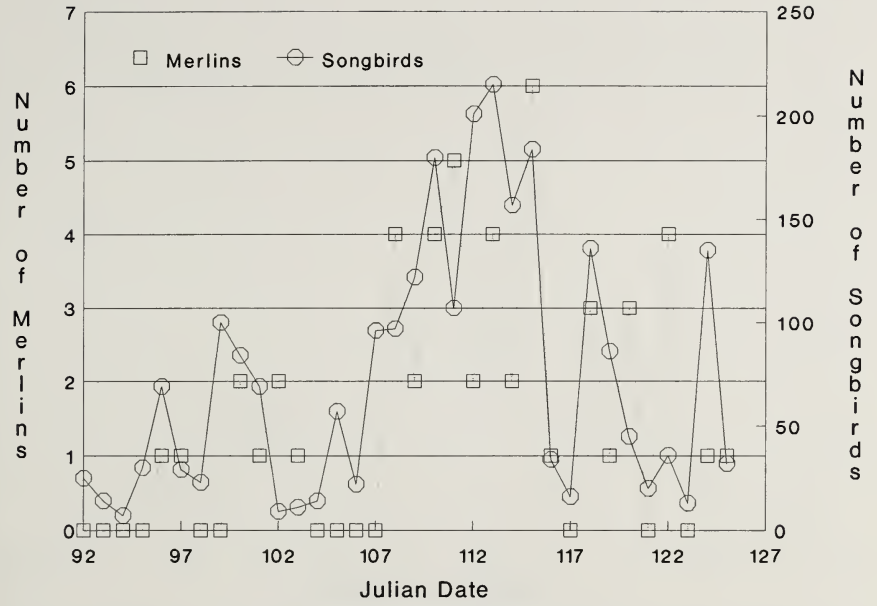

FIG. 1. Passage of Merlins and songbirds, E. Ship Island, 1991.

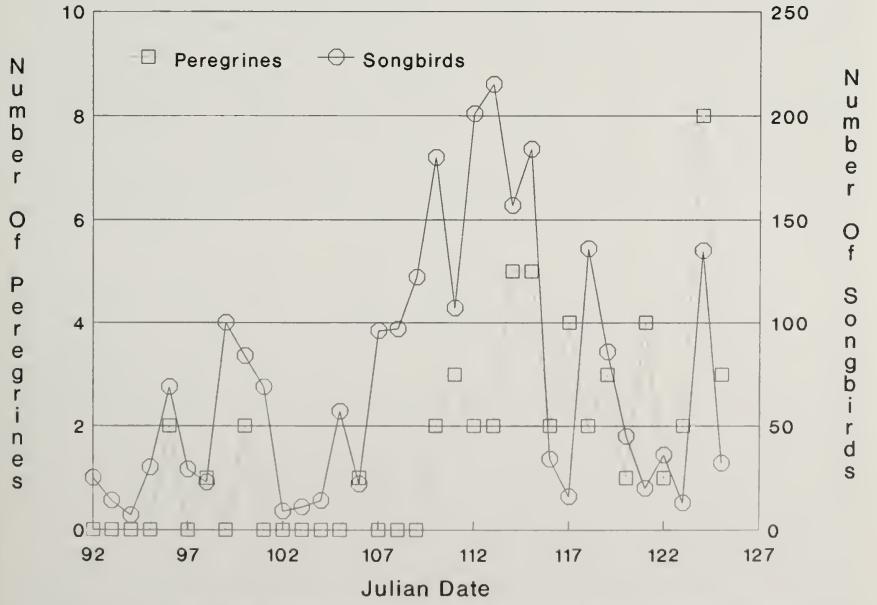

FIG. 2. Passage of Peregrine Falcons and songbirds, E. Ship Island, 1991.

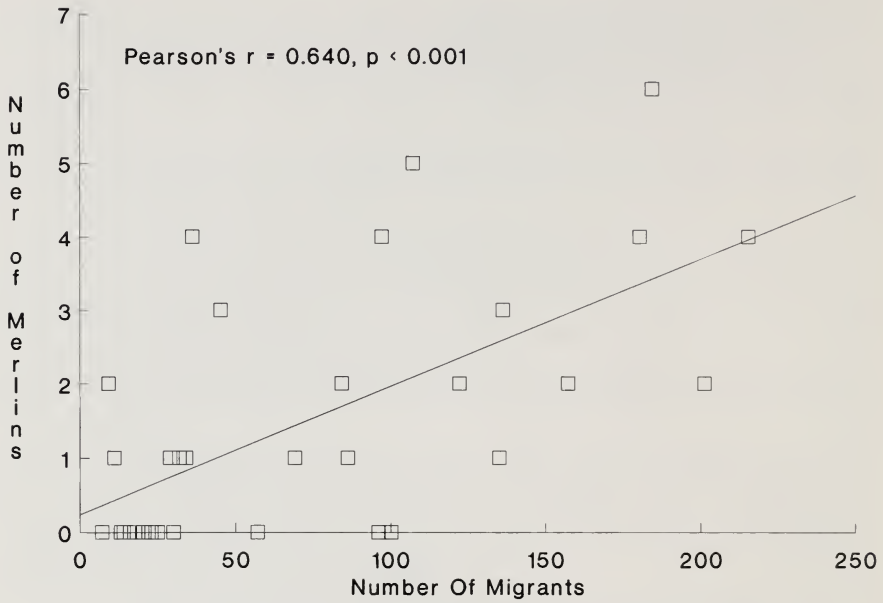

FIG. 3. Correlation between Merlin and songbird numbers, E. Ship Island, 1991.

ings coincided with the number of songbirds caught in mist-nets (Figs. 1 and 2). Pearson correlation analyses indicate that both Merlin and Peregrine Falcon numbers were correlated significantly with migrant numbers (Figs. 3 and 4). The coincidental timing of raptor migration with songbird migration could be explained by two hypotheses. First, hawks may be tracking a resource which is important to their survival during migration. Kerlinger (1989) has speculated that hawks may migrate along coastlines to take advantage of easily captured, energetically stressed prey. Raptors captured songbird migrants on East Ship Island: 14% of Merlins and 6% of Peregrine Falcons were seen attacking prey, and 8% of Merlins were seen with recently killed prey. Second, weather conditions that are favorable to songbird migration also are favorable for raptor migration. The correlation between Merlin and Peregrine Falcon numbers and songbird numbers on East Ship Island may also stem from a similar response to prevailing weather conditions. Both songbird migrants and Merlins take advantage of following winds when making water crossings (e.g., Nisbet 1970, Kerlinger 1989; see also Gauthreaux and Able 1970). The same headwinds or rain that force songbird migrants to "fallout" following trans-Gulf passage (Moore and Kerlinger 1987) may concentrate Merlin in the barrier islands along the northern coast of the Gulf of Mexico. Being stronger fliers, Peregrine Falcons may not be forced to land unless winds or storms are especially strong. This might explain why Peregrine Falcon sightings did not increase until the second half of the season (Fig. 2), whereas Merlin sightings were more evenly distributed (Fig. 1). It is also possible that the pattern observed for Peregrine Falcons is their typical timing of migration through this area.

Predation pressure is one of the many risks songbirds face during their annual migration, which must be balanced against their need to meet energetic demands. The Gulf coast barrier islands are important in helping songbirds to satisfy their energetic requirements, and in so doing, provide a resource for migrating raptors to do the same. The increase in predation

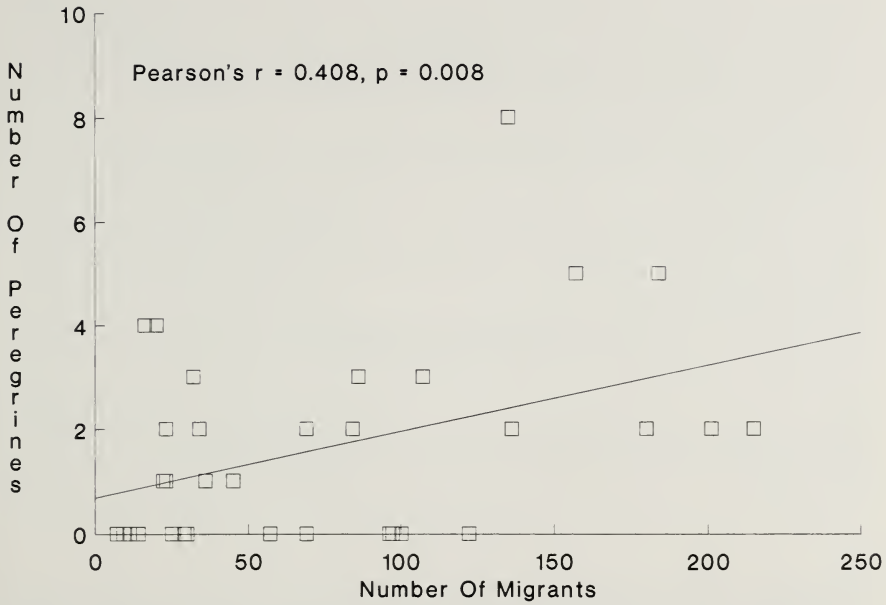

FIG. 4. Correlation between Peregrine Falcon and songbird numbers, E. Ship Island, 1991.

pressure may affect the foraging behavior and habitat use of songbird migrants, possibly delaying their arrival on the breeding or wintering grounds. Further investigations of raptor migration at stopover locations would prove valuable in understanding the relationship between songbirds and raptors during migration.

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Flight speeds of birds determined using Doppler radar.—We determined ground speeds of 12 species of birds (Table 1) in Jackson and Williamson counties in southern Illinois during the first two weeks of May 1991 using a Model K-15 Traffic Radar Unit (M.P.H. Industries, Chanute, Kansas). The unit has an internal calibration mechanism capable of maintaining and checking the accuracy of the digital circuitry. A tuning fork certified to oscillate at 1561 Hz was used for external calibration.

The objectives of our study were to (1) describe the correction factors required in using hand-held Doppler radar when obtaining flight speeds, (2) obtain measurements of non-migratory flight speeds of birds engaged in similar activities during the breeding season, and (3) relate these flight speeds to time of day, diet, foraging type, and roost type.

The K-15 Traffic Radar Unit uses a solid state Gunn Oscillator that generates radio energy in the microwave region. This energy is focused into a narrow beam and directed at the target at the speed of light. A portion of the beam is reflected back to the transmitter where a solid state mixer diode compares the frequency of the reflected beam to the transmitted frequency. The difference between the two frequencies is the Doppler frequency. The electronic circuitry then converts the Doppler frequency into a digital presentation of the target's speed.

Radar units are calibrated for direct line measurement of the speed of the target. If the target object approaches or recedes at an angle (this may involve deviations of azimuth, declination, or both), a portion of the motion will not be measured and recorded flight speed will be less than true speed. The magnitude of error increases as deviation(s) of azimuth and/or declination angle(s) increase.

The angle of azimuth (A) of the bird's flight path was determined with angles delineated on top of the radar unit. We discarded flight speeds of birds flying at an angle of greater than 10° either side of center. Angles of less than 10° produce less than a 1% error. To measure the angle of declination (B) we mounted a protractor on the side of the radar unit with a plumb line hanging from the center of the protractor. As the speed was recorded, the

TABLE 1
FLIGHT SPEEDS (M/SEC) OF BIRDS DURING DAYTIME AND EVENING

Species	Midday		Evening	
	N	Mean ± SE	N	Mean ± SE
Mourning Dove (*Zenaida macroura*)	7	9.88 ± 0.37	10	11.97 ± 0.75
Chimney Swift (*Chaetura pelagica*)	6	10.33 ± 0.50	10	12.26 ± 0.73
Purple Martin (*Progne subis*)	7	8.45 ± 0.41	8	11.09 ± 0.94
Cliff Swallow (*Hirundo pyrrhonota*)	9	9.83 ± 0.48	6	8.74 ± 0.50
Tree Swallow (*Tachycineta bicolor*)	9	10.02 ± 0.47	6	9.22 ± 0.57
Northern Mockingbird (*Mimus polyglottos*)	7	10.01 ± 0.21	4	9.30 ± 0.31
American Robin (*Turdus migratorius*)	8	7.22 ± 0.31	7	10.36 ± 0.75
Red-winged Blackbird (*Agelaius phoeniceus*)	5	10.02 ± 0.82	10	11.30 ± 0.75
Commnn Grackle (*Quiscalus quiscula*)	6	10.18 ± 0.16	9	11.71 ± 0.61
Eastern Meadowlark (*Sturnella magna*)	10	8.35 ± 0.31	5	12.02 ± 0.66
European Starling (*Sturnus vulgaris*)	7	9.95 ± 0.40	7	12.74 ± 0.86
House Sparrow (*Passer domesticus*)	10	10.21 ± 1.12	5	12.31 ± 1.10

line was pulled taut against the protractor and the angle was recorded along with registered speed. Values in m/sec were corrected for the angle of the bird's flight path relative to the radar unit's beam using the formula:

$$\text{Ground speed} = \text{recorded speed} \times 1/\cos(A) \times 1/\cos(B).$$

Measurements were obtained during two time periods: from 11:00 to 14:00 h CDST (midday period) and from 18:00 to 20:00 h CDST (evening period). We recorded 4–10 different birds for each species at each daily time period. All measurements were made on birds not in a state of alarm, flying at a distance of 10–60 m from the observer, and flying not over 20 m above the ground.

A two-way analysis of variance using the SAS GLM procedure (SAS Institute 1989) revealed significant species differences ($F = 4.40$; df = 11,154); $P < 0.001$), significant time period differences ($F = 29.24$; df = 1,154; $P < 0.001$), and a significant interaction term ($F = 2.52$; df = 11,154; $P < 0.01$). A Tukey/Kramer multiple-comparison procedure (Hinkle et al. 1988) revealed that, with the two time periods combined, Chimney Swifts and European Starlings (see Table 1 for scientific names) flew significantly faster than American Robins; measured flight speeds of the other species were not significantly different from one another. For four species measured (Purple Martins, American Robins, Eastern Meadowlarks, and European Starlings), ground speeds were significantly faster in the evening than at midday. While not statistically significant, measured speeds of three species (Cliff Swallows, Tree Swallows, and Northern Mockingbirds) were higher at midday than evening; these patterns of interspecific variation account for the significant interaction term. We also examined flight speed variation with regard to main diet (frugivore, aerial insectivore, and terrestrial insectivore), roost type (colonial, communal, and territorial), and style of flight (flapping and combination flap-glide). No statistically significant differences were found for any of these categories.

Ground speeds for the 12 species in this study showed considerable variability as indicated by the SE values. Schnell (1965, 1974), Tucker and Schmidt-Koenig (1971), Schnell and Hellack (1978, 1979), and McLaughlin and Montgomerie (1990) also report high variability

in measured ground speeds. Flying at minimum power velocity (Vmp) or maximum range velocity (Vmr) may be of less importance to birds flying at or near the nest area with abundant resources, than to birds on migration.

Non-migratory flight speed is determined by behavioral activities of birds and delimited by morphologic, physiologic, and aerodynamic constraints. Determination of flight speeds of birds in their daily habitat is necessary for closer examination of energetic costs of flight.

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Song variation within and among populations of Red-winged Blackbirds.—Evolution of micro-geographic song variation (e.g., dialects) and sizes of song repertoires continues to be a major interest, and comparative data from different populations of widespread species can help us understand the forces that produce such song variation. Because Simmers (1975) found no obvious differences in song of Red-winged Blackbirds (*Agelaius phoeniceus*) among New England sites, and because differences in song form and repertoire size are not substantial among northern, mostly migratory populations (e.g., Smith and Reid 1979, Yasukawa et al. 1980, Yasukawa 1981, Brenowitz 1983), we tested whether vocal behavior in two more southern and perhaps more sedentary populations, one in Florida and one in California, differed from northern populations.

Methods.—We recorded Red-winged Blackbirds at several sites. Our most intensive efforts were at Carr Lake, near Tallahassee, Florida, 22–29 April 1987. Most males had been banded with distinctive combinations of colored and aluminum bands. One male (male 17; see

Table 1) was recorded again five years later, on 21 April 1992. Supplemental recordings were made at three additional locations in Florida during April and May 1987 and April 1992: (1) St. Marks National Wildlife Refuge, about 60 km south of Carr Lake; (2) Orlando; and (3) Naples. Males were recorded in central California at three locations: (1) San Luis National Wildlife Refuge (near Los Banos), (2) Grizzly Island Wildlife Area (Fairfield), and (3) Gray Lodge State Wildlife Area (Gridley). Males at these secondary locations in Florida and California were not banded but were identified readily by their singing locations over a period of several hours.

We made most recordings with a Nagra IS-DT tape recorder and Sennheiser 106 microphone mounted in a 60-cm aluminum parabolic reflector. Supplemental recordings at Carr Lake and Naples and all of the recordings from Orlando were made with cassette tape recorders (Marantz PMD-221, Sony WMD6, or Realistic CTR-85) and a Sennheiser 816 shotgun microphone or Sony condenser microphone in a 33 cm Sony parabola. Occasional playback of a single song from a cassette recorder was used to stimulate singing from the males.

In the laboratory, song repertoires were analyzed with a Kay Elemetrics DSP5500 spectrum analyzer. Because males typically repeated a given song form several times before advancing to the next, males themselves provided a convenient measure for distinguishing variation within song types from variation among song types. Songs of a given male occurred as discrete types, with no continuous variation among the types, and repertoires could be identified. Each occurrence or series of a given song type, when separated by 10 or more songs of other types, was called a "bout," i.e., one "independent" occurrence of that particular song type.

To quantify differences in song among our Florida samples, we measured the rate of delivery of repeated units in the "trill" portion of the song. For most songs, the repeated units were discrete "syllables" clearly separated by silence from adjacent syllables (e.g., in Fig. 1; 9A, 9B, 11A), but in other songs the trill consisted of a rapid train of amplitude and/or frequency modulated pulses (in Fig. 1; 11B, 9C, 11D). For simplicity, we refer to this measure of repeated units as "syllables/second."

Results.—At Carr Lake, Florida, our estimates for song repertoires for 22 males ranged from four to eight types. Most males (12 of 22) sang five different types, and five males sang six types ($\bar{x} = 5.2$; see Table 1, Fig. 1). The number of sampled bouts for each male was sufficiently large that our repertoire estimates were largely independent of the sample size of total bouts recorded. Data from one male indicated that a song repertoire can be maintained intact from year to year. In April 1987, bird 17 used six song types; five years later, during April 1992, he was singing the same six types. In 11 recorded bouts during 1992, he used five types twice and his sixth one once. We could detect no between-year changes in the complex, multi-parted songs of this male.

We had fewer recordings from California, but the data suggested that repertoire sizes in California and Florida were not markedly different from each other. The four California males with the largest number of sampled bouts (12–16) each had four or five song types. Samples of only 12 bouts from each of the 22 Florida males also yielded four or five song types for 18 of the 22 males.

We found striking differences in the Red-winged Blackbird songs between two neighboring locations in Florida. A graph of one simple measure, the number of repeated syllables/sec in the song, was highly bimodal at Carr Lake. Of 122 different songs from the combined repertoires of all males (five songs were from males not listed in Table 1), 31 contained 8–18 syllables/sec (a "slow trill") and 89 contained >102 syllables/sec. Only two songs fell between these two groups, one at 62 and one at 72 syllables/sec. These distinctive "slow trill" songs comprised about one quarter of all song forms at Carr Lake and were sung by

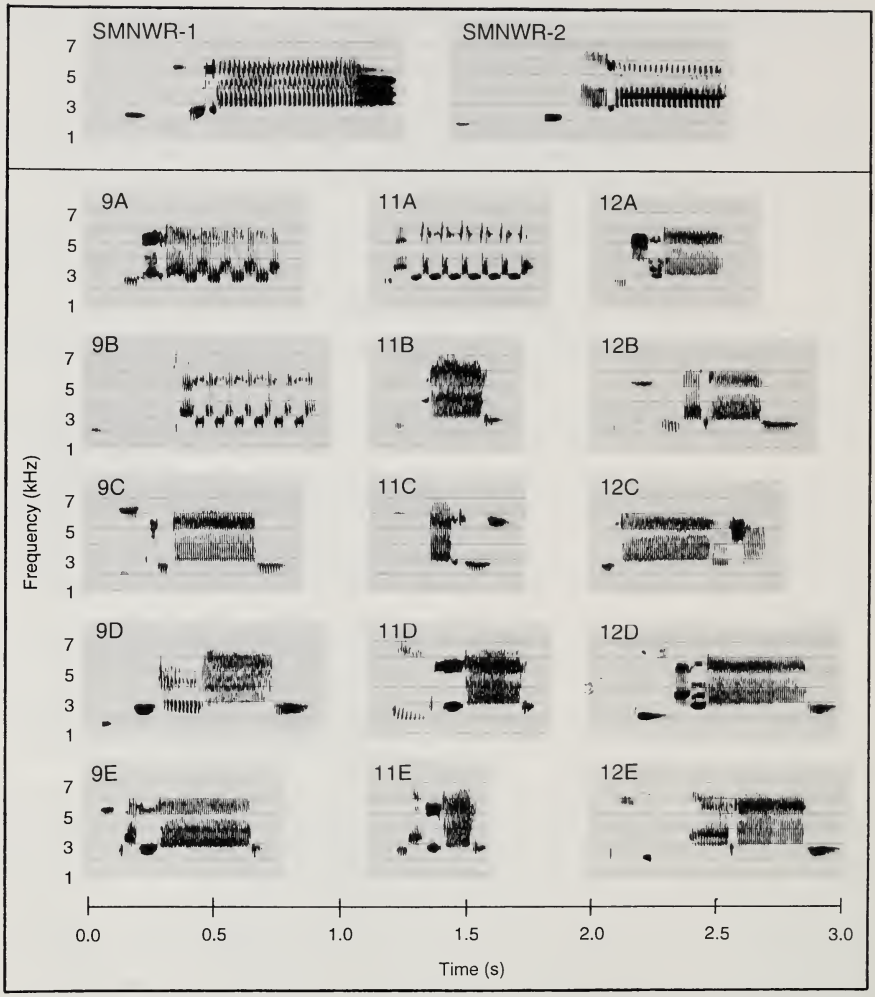

FIG. 1. Typical song repertoires for three male Red-winged Blackbirds (A–E for males 9, 11, 12) at Carr Lake, near Tallahassee, Florida, together with song types from two males at St. Marks National Wildlife Refuge (1 and 2, SMNWR), 60 km to the south. Carr Lake males typically had at least one or two song types with a relatively slow rate of syllable repetition (see 9A, 9B, 11A), but rates of syllable repetition in other songs were far more rapid. Many St. Marks refuge songs, however, such as the two illustrated here, had intermediate rates. Sonagrams were produced on a Kay Elemetrics DSP5500 sonagraph, with transform size of 100 pts (comparable to "wide-band" 300 Hz analog filter).

most (e.g., 18 of 22 intensively recorded males) of the birds there. At St. Marks Refuge, only 60 km south of Carr Lake and on the coast of the Gulf of Mexico, however, the structure of songs and the distribution of syllables/sec was markedly different (see Fig. 1). Of 38 recorded songs from about 25 individuals at St. Marks, six contained 8–18 syllables/sec

TABLE 1

SAMPLING EFFORT AND REPERTOIRE SIZE FOR 22 RED-WINGED BLACKBIRDS AT CARR LAKE, TALLAHASSEE, FLORIDA

Bird[a]	Number of bouts in which each song type was recorded[b]								Number of bouts recorded
1	7	7	6	4					24
2	17	10	9	7					43
3	15	13	12	11					51
4	6	5	3	3	2				19
5	4	3	3	3	2				15
6	6	5	5	4	2				22
7	10	10	7	7	6				40
8	7	6	5	5	4				27
9	10	9	8	8	7				42
10	12	10	8	7	6				43
11	19	9	8	8	6				50
12	16	12	10	9	5				52
13	10	7	6	6	5				34
14	8	7	5	3	1				24
15	10	8	8	7	5				38
16	5	4	4	3	3	1			20
17	6	6	4	3	2	2			23
18	6	6	4	4	2	2			24
19	9	9	6	6	4	4			38
20	6	5	4	4	3	3			25
21	4	3	2	2	1	1	1		14
22	10	9	8	8	8	7	7	2	59

[a] Birds listed in order of increasing repertoire size.

[b] Numbers of bouts for each male's song type (i.e., the number of independent occurrences for each type), listed in decreasing order. Thus, bird 1 sang four song types in 24 bouts; two types occurred on seven different occasions, one on six occasions, and one on four occasions.

(16% at St. Marks, 25% at Carr Lake), 23 contained 28–89 syllables/sec (61% at St. Marks, 2% at Carr Lake), and nine contained >100 syllables/sec (24% at St. Marks, 73% at Carr Lake).

Our recordings from other locations in Florida also revealed population differences in song. Of 20 songs from Orlando and 26 from Naples, none contained the characteristic slow trills found at Carr Lake and, to a lesser extent, at St. Marks. Of the 84 total recorded songs at locations other than Carr Lake, most songs (53, or 63%) contained 38–92 syllables/sec, thus falling between the two peaks of syllable repetition for Carr Lake males.

California males produced a greater variety of song forms than did the Florida birds, but discrete song types from each male could readily be identified. Some of the distinctive Grizzly Island songs (e.g., A and B, Fig. 2), for example, lacked a trill of identifiable repeated units and consisted largely of a few introductory notes together with a long nasal sound (E. S. Morton, unpubl. data). Some songs consisted of a series of relatively pure tones without a distinctive concluding trill, some contained a complex series of introductory notes with only an abbreviated concluding trill (C and D, Fig. 2), and still others contained two well-developed trills (E and F, Fig. 2). Each song form was given repeatedly and consistently, with the same kind of delivery as that used by males of other populations. We therefore

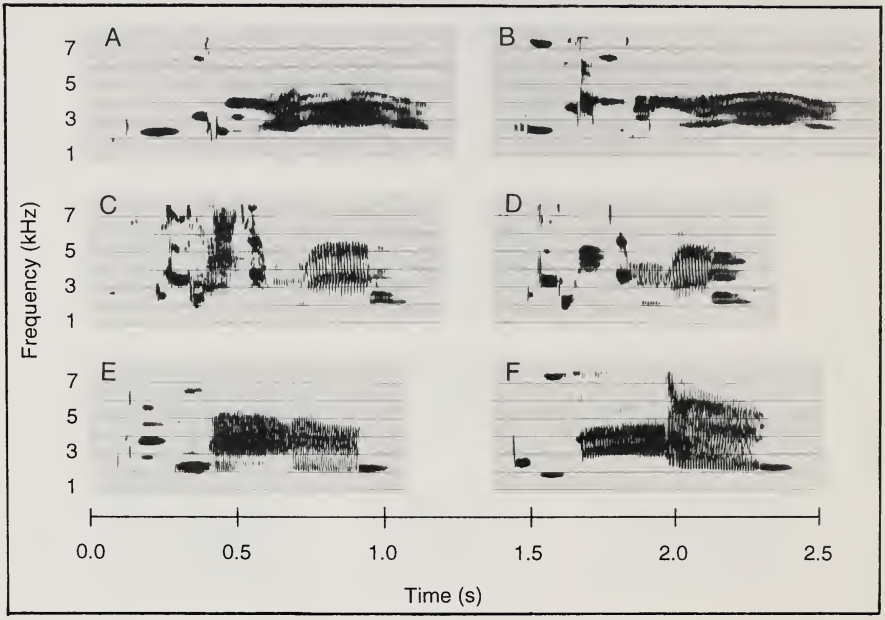

FIG. 2 Geographic variation of songs in California populations. Males within a given population shared similar songs (A and B from Grizzly Island, Fairfield; C and D, E and F from San Luis National Wildlife Refuge, Los Banos), thus resulting in local dialects.

classified each of these song forms as a type within a male's repertoire (cf Morton, unpubl. data).

Although the variable structure of songs prevented us from consistently using features such as syllable rates to demonstrate geographic variation within California, qualitative differences in the songs from location to location were obvious, even to the unaided ear. As in our Florida populations, neighboring males within in California populations often shared similar song types (see Fig. 2). Additional surveys by Morton (unpubl. data) in some of these areas revealed abrupt changes in song form over distances of less than 1 km.

Discussion.—The average or median repertoire size of songs of males in local populations of Red-winged Blackbirds seems to be four or five. The two largest samples of published repertoires are from central Indiana, where males sing two to eight song types ($\bar{x}$ = 3.9, median = 4, N = 49 males; Yasukawa et al. 1980), and from southeastern New York, where males sing three to eight types ($\bar{x}$ = 4.8, median = 5, N = 34 males; Yasukawa 1981). The majority of Florida birds, and probably California birds also, had repertoires of four or five types.

Most authors (e.g., Kirn et al. 1989) have inferred that Red-winged Blackbirds are "open-ended learners" and can change the composition or increase the size of their repertoire with age, but our data from one Florida male suggest that additional data are needed on this topic. In the laboratory, first and second year males are able to learn songs (Marler et al. 1972, Kroodsma, unpubl. data), but males typically do not breed until they are two years old (Orians 1980). In the field, older breeding males seem to have larger song repertoires than do younger breeding males (Yasukawa et al. 1980), but this difference could arise

without learning if birds with larger repertoires have greater survival rates (Lambrechts and Dhondt 1986, Hiebert et al. 1989). Field data from Carr Lake male 17 reveal that a repertoire of six songs can be maintained intact over a period of five years. Stability in song form from year to year was also reported by Simmers (1975).

We are not able to compare the extent of micro-geographic song variation in our Florida and California samples with those of more northern populations. Although the basic form of the *konk-la-reeee* song pattern seems relatively constant over broad areas of the eastern United States (Marler et al. 1972, Simmers 1975, Smith and Reid 1979, Yasukawa et al. 1980, Brenowitz 1983), no quantitative survey such as we used in Florida has been attempted. Song forms in the eastern United States certainly do not change as dramatically over distance as do the songs of California males (Morton, unpubl. data; Brenowitz 1983), but changes nevertheless might occur, perhaps in more subtle aspects of the song.

The apparent local differentiation in songs among populations in California and Florida in relation to that of more northerly populations may be a consequence of the fact that northern populations are highly gregarious in winter. Migratory red-wing populations undoubtedly mix in migration and in the massive southern winter roosts formed mostly by males (Burtt and Giltz 1977, Dolbeer 1978). Although adults can be highly site faithful from one season to the next (Yasukawa et al. 1980, Beletsky and Orians 1987), the extensive mixing of populations from different breeding sites probably contributes both to relatively high dispersal distances, perhaps especially by first-year male birds (Knittle et al. 1987), and to a relatively high gene flow among populations (Cox and James 1984, Ball et al. 1988, Gavin et al. 1991). Males do sing in these large flocks (pers. obs., and Brenowitz 1981), and any song learning by first or second year males (Marler et al. 1972), and especially by adults, would lead to song similarities over the breeding range represented by the flock. Birds of our Florida and California sites flock less in winter than do those blackbirds of most previous studies. In northern Florida, data from measurements of birds in both breeding season and winter suggest that males are sedentary, although females migrate (James et al. 1984). Birds of central California also appear to be resident the year round (Van Rossem 1926). The more sedentary behavior of the males would lead to increased vocal isolation of populations and an increased degree of local song variation.

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Nest site selection by birds in Acacia trees in a Costa Rican dry deciduous forest.—Little is known about the criteria that tropical birds use to choose nest sites because the spatial complexity of tropical forests allows birds to conceal nests effectively (Skutch 1976). Nests in dry forests are easier for researchers to find and identify than those in wet forests because

trees in the former habitat drop their leaves during the dry season. In a dry forest at Palo Verde National Park, Costa Rica, three species of birds commonly build nests in swollen-thorn acacia trees (*Acacia* spp.): Rufous-naped Wren (*Campylorhynchus rufinucha*), Yellow-olive Flycatcher (*Tolmomyias sulphurescens*), and Streaked-backed Oriole (*Icterus sclateri*). Two species of acacia are found at Palo Verde: *Acacia cornigera,* which occurs in wet or seasonally flooded areas, and *A. collinsii,* a more widespread species found in drier areas. Three species of *Pseudomyrmex* ants live in a mutualistic association with these two *Acacia*: *P. spinicola* (a more aggressive species; Janzen 1966, Young et al. 1990), *P. flavicornis* (less aggressive), and *P. nigrocinta* (occurring on younger *A. collinsii* trees). These ants typically clear a large area, or halo, around one or several acacia trees to defend the plant from potential competitors (Janzen 1966). Two of the three bird species mentioned above (wren and flycatcher) appear to nest almost exclusively in ant-acacias. In Guatamala, Gilardi and Von Kugelgen (1991) described what appeared to be a commensal relationship between two species of Acacia-nesting birds: White-bellied Wrens (*Uropsila leucogastra*) and Yellow-olive Flycatchers. The ants most likely provide the birds with protection from nest predators (Janzen 1969, 1983: p. 763). Young et al. (1990) found that Rufous-naped Wrens nest in Acacia trees occupied by *P. spinicola* twice as often as expected by chance, and that ants occupying trees with Rufous-naped Wren nests were more aggressive than those ants found in trees containing the nests of other species of birds.

We speculated that birds may use some of the characteristics of the acacia trees and their halos as cues to select nest sites. Specifically, we examined nest sites to see whether (1) birds demonstrated a preference for specific species of acacia, (2) birds showed a preference for one species of ant over another, (3) the height and diameter of a tree affected nest site selection, and (4) size of the acacia halo affected nest site selection.

We searched for bird nests by walking foot trails and roads near Palo Verde Biological Station (9466 ha, 10°N, 85°W), Guanacaste Province during February 1993. We identified bird species by nest architecture: Rufous-naped Wrens build dense spherical nests; Yellow-olive Flycatchers build small pendant nests; and Streaked-backed Orioles build relatively larger pendant nests with a narrower attachment to the supporting branch (hereafter birds are referred to as wrens, flycatchers, and orioles). None of the three species of birds nest during the dry season (Stiles and Skutch 1989), but all three build sturdy nests which last from one season to the next. Unlike the other two species, wrens may build several nests during a breeding season, using some for roosting and others as possible dummy nests to distract predators (Collias and Collias 1964, Janzen 1983: p. 559). Thus, relative percentages of observed nests do not necessarily reflect the abundance of the three species. We identified *Acacia* species (*A. collinsii* or *A. cornigera*) and species of ant occupying the tree where ants were present. Trees shorter than 1 m were not included because nests are rarely found in such trees and were not observed in this study. We recorded tree diameter at breast height (dbh), height of tree, height of nest in tree, size of acacia halo (length × width), and number of ≥ 1 m tall acacia trees within the halo. To account for variations in halo shape, halo area was calculated as the longest length × the longest perpendicular width of the halo.

We used a variety of statistical tests to determine which ecological factors these three species of birds used to choose nest sites. We performed one-way analyses of variance (ANOVAs) to assess the significance of tree height and paired *t*-tests for tree dbh. Because halo area and number of trees within a halo were not normally distributed, we used Kruskal-Wallis non-parametric tests to examine their significance in nest site selection. We used Chi-square tests for homogeneity to assess whether the proportion of nests built in trees with a particular species of ant, and in a halo with varying numbers of trees, was uniform across bird species.

We found 52 wren (80%), eight flycatcher (12.3%), and five oriole (7.7%) nests. All wren, oriole, and five flycatcher nests were in *Acacia collinsii.* We also found two flycatcher nests

Table 1

Nest Site Characteristics of Birds Nesting in Acacia Trees in Palo Verde National Park, Costa Rica, 1993, Including Total Number of Nests, Mean Height of Nests and Trees, Mean Number of Trees/Halo, and Mean Halo Area by Bird Species

Parameter[a]	Rufous-naped Wren (N = 52)	Yellow-olive Flycatcher (N = 8)	Streaked-backed Oriole (N = 5)
Mean nest height (m)	4.1 (±1.5)	3.8 (±1.1)	6.5 (±2.3)
Mean tree height (m)	6.2 (±1.5)	8.9 (±5.7)	8.0 (±2.0)
Mean number trees per halo	7.7 (±8.4)	2.1 (±3.2)	4.4 (±6.1)
Mean halo area	20.4 (±32.5)	3.3 (±9.4)	6.4 (±12.1)
Mean DBH	5.0 (±1.5)	6.3 (±1.6)[b]	4.3 (±1.4)

[a] All parameters are reported as are means ± one SD.
[b] DBH for Yellow-olive Flycatcher are reported only for *Acacia collinsii* trees.

in *Calycophyllum candidissium* and one flycatcher nest in *Brosimum alicastrum*. Of wren nests found, 85% (N = 44) were in acacias occupied by *P. spinicola*, 11.5% (N = 6) were in trees occupied by *P. flavicornis*, and 4% (N = 2) had no ants. Only half the flycatchers nests were found in trees with ants (N = 3 with *P. spinicola* and N = 1 with *P. flavicornis*) while 60% of oriole nests were in trees with ants (N = 2 with *P. spinicola* and N = 1 with *P. flavicornis*). The proportion of flycatcher and oriole nests built in trees occupied by *P. spincola* was significantly lower ($\chi^2 = 18.58$, df = 4, $P < 0.001$) than wrens. To assess the relative criteria which the three species of birds may use to select nest sites, we compared the characteristics of trees and halos with nests among bird species. Orioles placed their nests significantly higher in trees than either wrens or flycatchers ($F = 6.01$, df = 64, $P < 0.05$; Table 1). Bird species differed significantly in the height of the tree in which they placed their nests ($F = 5.13$, df = 64, $P < 0.05$; Table 1). Wrens chose trees that were significantly shorter than trees chosen by flycatchers, but there were no differences between wrens and orioles or between flycatchers and orioles (Bonferroni pairwise comparison, $t = 2.46$, ns). Flycatchers and orioles nested in trees with significantly different diameters at breast height ($t = 3.38$, df = 4, $P < 0.05$; Table 1). There were no significant differences between the dbh of the trees wrens placed nests in and the trees in which flycatchers and orioles nested (Table 1).

Halo characteristics were more important criteria for wrens than for the other two species. Wrens chose trees with halos three times and six times the size of orioles and flycatchers, respectively (KW = 13.1, $P < 0.001$, Table 1). Furthermore, wrens chose halos containing significantly more acacia trees than the other two species (KW = 6.28, $P < 0.05$, Table 1).

Wrens built their nests in shorter trees and placed their nests lower in trees than did either flycatchers or orioles. Further, they chose larger acacia halos with more trees than did the other two species. Wrens also built the majority of their nests in trees with the more aggressive *P. spinicola*. These results support the findings of Young et al. (1990) that ant activity is an important criteria to nesting wrens and that dbh of nest trees were not different between wrens and other species.

Pendant nests generally provide greater protection from nest predators than do spherical nests; pendant nests can be placed at the end of thin branches that are difficult for many predators to reach and that provide the nesting bird with an early warning of a predator's approach (Skutch 1976). One explanation for the wren's greater affinity for ant-protected

acacias is that, based on nest architecture alone, its nests may be more vulnerable to predation than are flycatcher or oriole nests. By placing nests in ant-protected acacias, the wren presumably gains additional security for its eggs and nestlings. This may explain why halo characteristics are more important to wrens than to the other two species. These data suggest that larger and more dense halos with high *Pseudomyrmex* activity are the most likely signals which wrens use to assess optimal nest location.

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Notes on the ecology and population decline of the Rota Bridled White-eye.—The Bridled White-eye (*Zosterops conspicillata*) of the Mariana Islands is represented on Rota by the endemic subspecies *Z. c. rotensis,* which once was common and widespread (Baker 1951, E. Taisacan, pers. obs.), but by the 1960s had become uncommon (Engbring et al. 1986). In 1982 the total population, by then restricted to the Sabana plateau region, was estimated at 10,763 compared to 229,138 (*Z. c. saypani*) for the similarly sized island of Saipan (Engbring et al. 1986). J. Engbring (pers. comm.) estimated a further 26% decline on Rota by 1987, although he believed poor weather may have interfered with censuses. By 1991, qualitative but intensive distributional surveys by E. Taisacan and G. Witteman yielded

population estimates of <300–1500. Hence, from 1982 to 1991, populations appeared to decline by at least 87%. Furthermore, E. Taisacan (pers. obs.) found that from 1988 to 1991 maximum flock size dropped from 23 to ca ten. Craig (1989) has reviewed literature that links population declines in Bridled White-eyes to decreasing flock size.

Because the Rota Bridled White-eye is now rare, we gathered new data on its social behavior, foraging, and microhabitat use to document aspects of its ecological requirements. We also report results of monthly estimates of population density in the heart of its present range and offer insights into reasons for its population decline.

Methods.—From 1990–1992, we observed social behavior, foraging, and microhabitat use in the same manner employed by Craig (1990) for white-eyes on Saipan. Briefly, this entailed recording for each foraging attempt the (1) portion of the tree chosen, (2) surface used, (3) method employed, and (4) size of perch used. Qualitative observations were made on social behavior. In addition, E. Taisacan conducted monthly variable circular plot (Reynolds et al. 1980) censuses (33 total points separated by 150 m, 8 min counts/point) along J. Engbring's (pers. comm.) 1987 transects four and ten in the Sabana region. Censuses were made from June 1990–January 1991 and are compared with the identically performed censuses of January–August 1989. Pooled raw data from the two transects (made comparable by computing birds detected/10 census stations) are reported here.

Results and discussion.—Rota Bridled White-eyes were found as isolated flocks occurring solely on the Sabana plateau at ca 400–490 m elevation. All flocks occurred in native forest, although the character of the forest varied from stunted, open forest on the plateau summit to closed, mature forest on the upper Sabana slopes. Dominant trees within the range of the white-eyes included *Elaeocarpus joga, Ficus prolixa, Intsia bijuga, Guettarda speciosa, Pisonia umbellifera, Claoxylon marianum, Pandanus* spp., and *Hernandia labrynthica.*

Based on the frequent food begging observed, flocks appeared to be composed of related individuals. Incidental observations and census data (flock detected at adjacent points on different censuses) suggested that flocks used areas at least 150 m in diameter. We always found flock members in the same vicinity and found no birds in identical habitat between existing flocks. Flocks appeared to have a maximum of ten individuals, although small groups of two to three birds were seen often. These observations indicate that Rota Bridled White-eyes are relatively sedentary, inhabit a home range, and live in family groups or extended families.

Although sample size was small (24 observations), quantification of foraging activities showed that Rota Bridled White-eyes were generally similar to the Saipan population in their foraging behavior and microhabitat use (Table 1). Like Saipan birds (Craig 1989), those on Rota foraged mostly in the tree crown where they gleaned insects from leaves. Moreover, they predominantly chose perches <1.0 cm diameter for foraging, i.e., those small branchlets making up the majority of outer tree crowns.

Census data from 1989 and 1990–1991 showed a statistically non-significant ($r^2 = 0.07$) trend toward declining counts (Fig. 1). However, the trend is consistent with our qualitative impression that populations continue to decline. Moreover, Engbring et al.(1986) found 40.0 birds/10 stations at 66 Sabana census points, whereas during this study we averaged 8.6 birds/10 stations at 33 census points. The weak statistical relationship we found is likely attributable to the large inherent variation in census data. Taking into account those months in which no censuses were made, the equation for population decline is: census detections = 9.931 − 0.102 month, where month = the number of months after January 1989 (January 1989 = 1).

Several agents, particularly disease and introduced predators, have been implicated in causing population collapses of birds on Pacific islands (van Riper III et al. 1986, Savidge 1987). However, no evidence links disease to bird declines on Guam in the Mariana Islands

TABLE 1

COMPARISON OF FORAGING BEHAVIOR AND MICROHABITAT USE BY SAIPAN[a] AND ROTA BRIDLED WHITE-EYES

	Population			
	Saipan		Rota	
Behavior/microhabitat	Percent use	N	Percent use	N
Tree zone				
Top	72.0	103	83.3	20
Middle	25.9	37	16.7	4
Lower	2.1	3	0	0
Foraging surface				
Leaf/bud	84.4	119	79.2	19
Flower	6.4	9	0	0
Fruit	1.4	2	4.2	1
Branch/trunk	7.8	11	16.7	4
Foraging method				
Glean	89.0	130	100	24
Probe	6.2	9	0	0
Hover/sally	4.8	7	0	0
Perch size (cm)				
<1.0	75.5	37	87.0	20
1.0–<2.0	12.2	6	13.0	3
2.01–>4.0	12.2	6	0	0

[a] From Craig 1990.

(Savidge 1986). Predation by the introduced brown tree snake (*Boiga irregularis*), responsible for the extinction of forest birds on Guam (Savidge 1987), also appears unrelated to the Rota Bridled White-eye decline because the snakes are unknown on Rota. Instead, the predatory Black Drongo (*Dicrurus macrocercus*), introduced on Rota in 1935 (Baker 1951), is implicated in causing the population declines of several native bird species.

Black Drongos did not become abundant until the 1960s (E. Taisacan, pers. obs.), the time when the decline in Rota Bridled White-eye populations was first noted. Maben (1982) demonstrated that introduced Black Drongos on Guam preyed on small passerines, although she believed drongos had little effect on their populations. Despite this belief, the present distribution of Black Drongos on Rota shows a negative relationship with that of white-eyes, which are now found mostly in extensive stands of native Sabana forest. Engbring et al. (1986) found Drongos abundant in lowlands (40–42 bird/10 stations), and particularly in open habitat, but uncommon in the forest of the Sabana plateau (15 birds/10 stations). The Rota Bridled White-eye appears particularly susceptable to predation by Black Drongos because it is very small and feeds in exposed microhabitats. Like the Saipan subspecies, it is a flocking, vocal bird that forages in the forest canopy and flies above the forest (see Craig 1989, 1990).

Notably, all birds on Rota too large for drongo predation are abundant and widespread (Engbring et al. 1986). Only the small Rufous Fantail (*Rhipidura rufifrons*) is also uncommon.

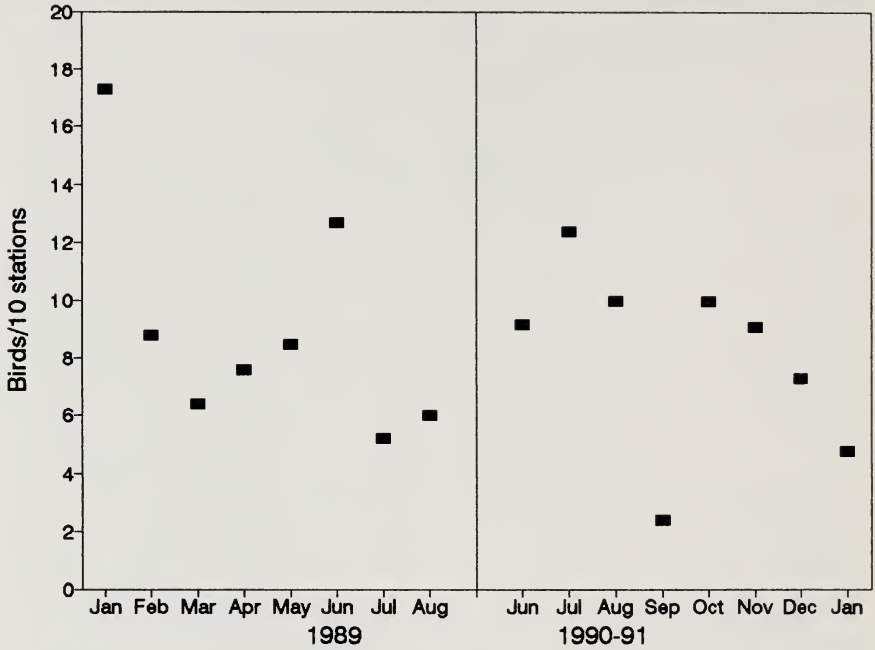

FIG. 1. Population densities of Rota Bridled White-eyes based on transect counts. Data are from January–August 1989 and June 1990–January 1991.

Baker (1951) reported Rufous Fantails as common on Rota, but by 1982 Engbring et al. (1986) found that they occurred less densely on Rota than on Saipan, Tinian, and Aquijan, where drongos are absent. Rufous Fantails are also preyed upon by Black Drongos (Maben 1982). However, they are likely less susceptable to avian predation than white-eyes because they are territorial (thus spread out) and forage in the forest understory.

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Notes on the natural history of the Crescent-faced Antpitta.—The Neotropical antpittas (Formicariidae) are renowned for being secretive and poorly known, and the Crescent-faced Antpitta (*Grallaricula lineifrons*) remains the most enigmatic of its genus. Prior to our recent Ecuadorian avifaunal investigations, this boldly marked antpitta was known from only the type locality, Oyacachi, Prov. Napo, on the east slope of the Andes in Ecuador (Chapman 1924), and from two records from Puracé National Park, Depto. Cauca, on the west slope of the Central Andes in Colombia (Lehmann V. et al. 1977). Our observations substantially add to the knowledge of this species' natural history and dramatically increase its known range.

Distribution and status.—On 19 August 1991, Ridgely and Sornoza encountered a female (ANSP 184002) north of Taday, Prov. Cañar, in humid temperate forest at ca 3000 m elevation (02°34′S, 78°43′W; Fig. 1). In 1992, *G. lineifrons* was found at two additional localities along the eastern slope of the Ecuadorian Andes (Fig. 1). From 14–24 March, it was fairly common between 3225 and 3400 m in humid, temperate forest along the western slope of Cerro Mongus in extreme eastern Carchi (00°27′N, 77°52′W; Robbins et al., in press). During a brief period of fieldwork, 28 March–1 April, in the Cordillera de Cordoncillo, Prov. Loja (03°41′S, 79°13′W; Fig. 1), Robbins, Rosenberg, and Sornoza located three birds at 3100 m in disturbed montane forest connected to primary forest. At this latter locality, Krabbe heard birds singing on 2 September and 6 November 1992.

The fact that only four of eighteen individuals have been located without the aid of voice or the use of mist-nets attests to why this fairly common antpitta has been overlooked. It is now apparent that *G. lineifrons* is distributed widely between 3000 and 3400 m along much of the eastern Ecuadorian Andes from near the Colombian border (undoubtedly it occurs along the adjacent eastern slope in Colombia) south at least to northern Loja. Historically, the upper Río Zamora may have been a barrier to this species' dispersing farther south, as Parker et al. (1985) failed to find it in northern Peru. Despite "trolling" with prerecorded tapes Robbins, Ridgely, and Sornoza did not encounter it in the Cordillera Lagunillas (04°47′S, 79°24′W) in extreme southern Ecuador in 1992 (ANSP/MECN, unpubl. data). The Río Zamora appears to be a barrier to the dispersal of other montane avian taxa, e.g., *Oreotrochilus* complex, *Metallura odomae/M. baroni,* and *Anairetes agilis.*

At the Cerro Mongus locality, nine individuals (6 specimens; 5 study skins, 1 skeleton; ANSP, MECN) were recorded along ca 3 km of forest trails. Three birds (presumed pair,

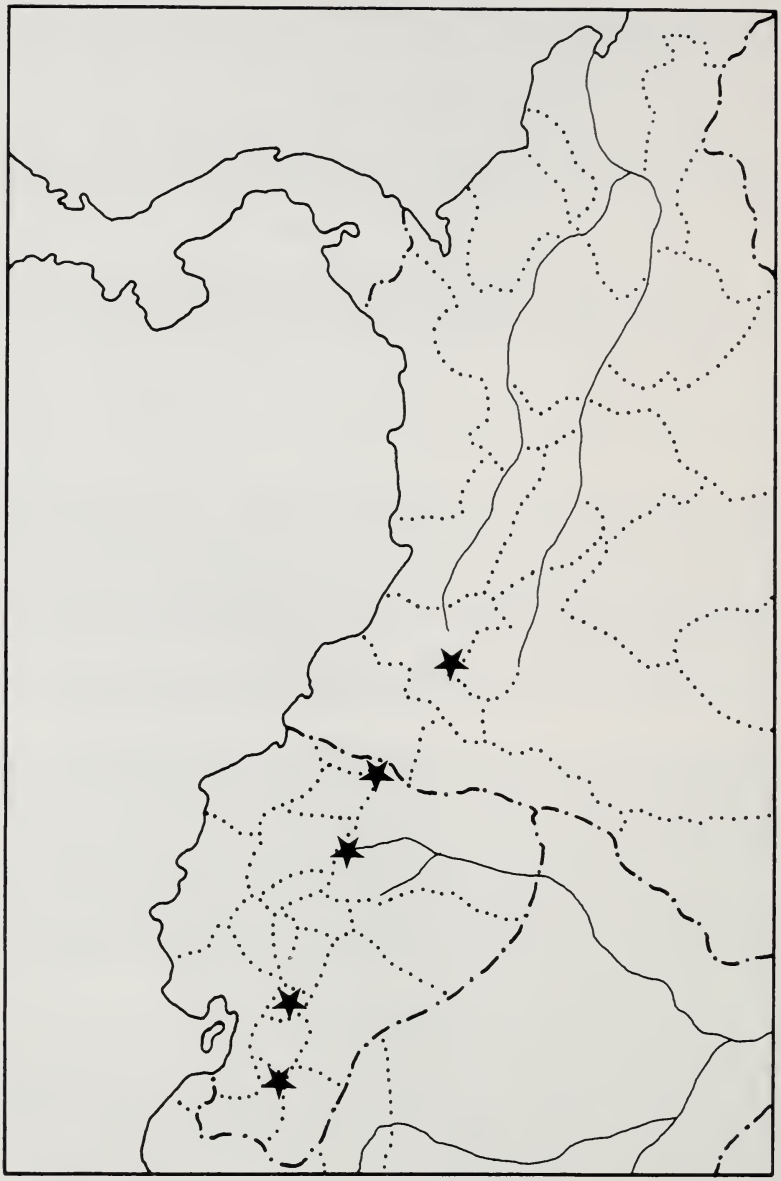

FIG. 1 Known localities of the Crescent-faced Antpitta (*G. lineifrons*).

ANSP 184707-8, and another singing individual) were located along ca 2 km of disturbed forest trail at the Cord. Cordoncillo site. We believe that the above antpitta numbers are underestimates because we worked these areas outside the peak of the breeding season (see below), when we presume this antpitta vocalizes more frequently.

This species was encountered principally in dense understory in ravines of taller, undisturbed forest, although two individuals were encountered in secondary forest connected to primary forest. Birds invariably were seen perched on moss-laden tree limbs and bamboo vines 1–4 m above the ground. Wing-flicking individuals responding to tape playback were seen making short flights, usually less than 1 m, between perches. Birds rarely perched on any limb for more than a few seconds, occasionally clinging sideways to mossy limbs and vines as is typical of the species' congeners. After tape playback, birds occasionally perched for up to 20 seconds on horizontal limbs. Although bamboo (*Chusquea* sp.) was conspicuous in most birds' territories, there were no dense stands of it, and in a couple of territories it was scare.

Morphology.—Based on our series of six adult specimens (4 males, 2 females; none with bursa; skull ossification >90%) there is no obvious sexual dimorphism. In addition, an immature male (ANSP 184706) and female (ANSP 184002) that had skull ossifications of 75%, 70%, respectively, and bursa (4 × 3, 3 × 2 mm, respectively) are indistinguishable in plumage from the five adult birds. Only the subtropical Ochre-fronted Antpitta (*G. ochraceifrons*) and Peruvian Antpitta (*G. peruviana*) are sexually dimorphic in this genus (Graves et al. 1983; Parker et al. 1985). However, a juvenile male specimen (ANSP 184703; bursa 4 × 4 mm; sk. oss. 20%) differs from the adults in the following characters: its hindcrown and nape feathers are a fluffy, dull reddish-brown, quite similar to juveniles of other *Grallariculas* (e.g., ANSP specimens of Ochre-breasted Antpitta [*G. flavirostris*]). The olive-green back and the streaked underparts also are mixed with a few of the dull reddish-brown feathers. The abdomen is lightly washed with buff.

From our relatively small sample size (N = 9), males do not differ significantly from females in culmen, wing and tail length, nor in mass (2-tailed, *t*-test; $P < 0.05$). Pooled sexes gave the following means (± SD) in mm: bill (culmen from base), 16.2 (± 0.5); wing (chord), 77.1 (± 1.7); tail (central rectrix), 37.7 (± 1.3); tarsus, 27.8 (± 0.4); and mass (g), 21.1 (± 0.7).

Soft-part colors of the eight adult plumaged specimens were described by the preparators as: irides brown or dark brown; bill black or with extreme base of mandible pallid yellow; tarsi and feet gray, bluish-gray, purplish-gray, or vinaceous gray.

Vocalizations and breeding condition.—Adult males were recorded giving a slightly ascending series of closely spaced notes (Fig. 2A). One male recorded under natural conditions consistently gave 21 notes per song bout, whereas males responding to playback gave 13 to 15 notes per bout. The duration of the male's song under natural conditions was ca 3.5 seconds, with a frequency range of 2.6 to 3.9 kHz. An adult female (ANSP 184707) gave the primary song after her presumed mate was collected. Both sexes gave a single-noted, slightly down-slurred whistle (Fig. 2C); this call note is similar to that given by *G. flavirostris* (Robbins and Ridgely 1990). On 22 March 1992, at the Cerro Mongus site, Krabbe and Sornoza observed and recorded a juvenile male (ANSP 184703) give a song that is similar to the adult's song, except that the notes were more raspy and much lower in frequency (Fig. 2B)

Unsolicitated singing was very sporadic and primarily restricted to brief periods (1–2 songs) in the early morning and at dusk at the Cerro Mongus and the Cord. Cordoncillo sites. Birds responding to tape playback silently approached and sang only occasionally. The relatively low level of song delivery, the gonad information (lg. testis was 4 × 2 mm; lg. ovum 1 mm), molt stage (adults were either molting or in fresh plumage), and the presence of a juvenile and two immatures indicate that the primary breeding season occurred prior to our March work at Cerro Mongus and the Cord. Cordoncillo. Using a prerecorded tape Ridgely, Sornoza, P. Greenfield, and T. Davis were able to stimulate two individuals to sing on 13 June 1992 at the Cerro Mongus site. Bret Whitney failed to hear this species, without

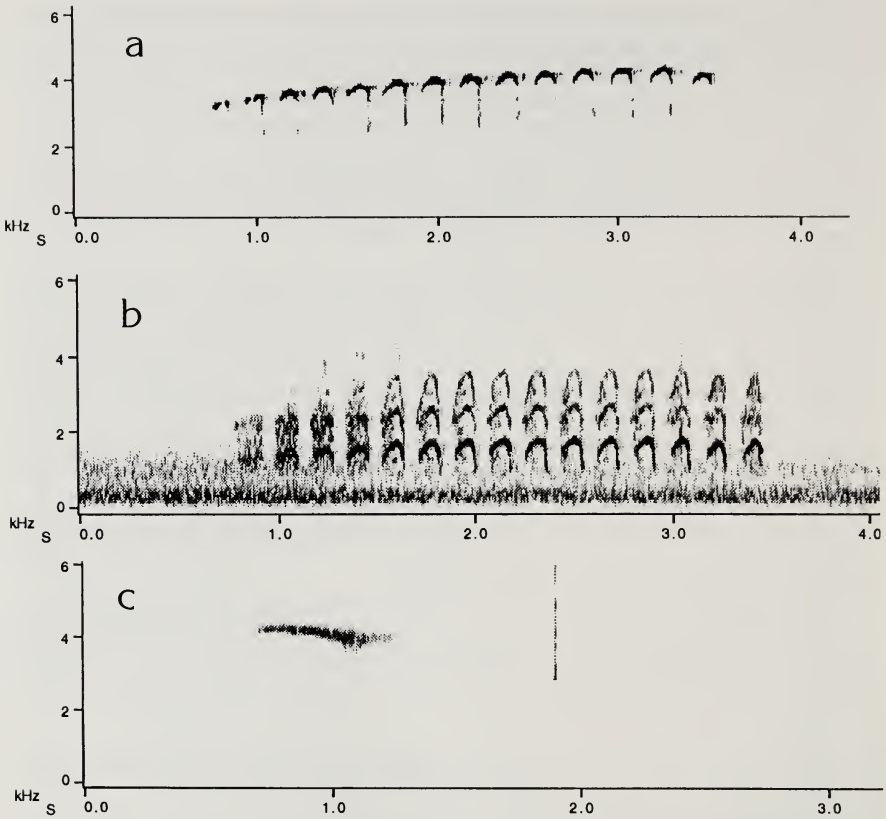

FIG. 2. Spectrograms of *Grallaricula lineifrons*' vocalizations. A) adult male song, 14 March 1992, recorded by M. B. Robbins; B) juvenile male song, 22 March 1992, recorded by N. Krabbe and F. Sornoza, the top two series of dark figures are harmonics; C) call note, 30 July 1992, recorded by B. M. Whitney. All recordings were made after playback at Cerro Mongus, Prov. Carchi, Ecuador.

the use of a prerecorded tape, during a visit to Cerro Mongus on 30 July 1992. The area was very dry during his visit, and the local people related that they badly needed rain.

Based on the August Cañar bird's skull ossification (70%) and the presence of a bursa (3 × 2 mm), as compared to a March bird from Cerro Mongus (ANSP 184002) with similar ageing characteristics, it appears that the Cañar bird fledged a few months after the Cerro Mongus individual. As with many temperate zone inhabiting species, *G. lineifrons*' breeding season appears to be correlated positively with the season of greatest rainfall, i.e., from Oct./Nov. to Jan./Feb.

Diet.—The stomach contents of all nine specimens contained insect fragments. Identified stomach contents of three adults were as follows. Cerro Mongus male (ANSP 184705): beetle fragments (Coleoptera), including at least two adult weevils (Curculionidae) and a large beetle larva (not Curculionidae); Cerro Mongus male (ANSP 184704): one Homoptera

(probably Membracidae), one Coleoptera larva (probably Elateridae), one adult Curculionidae, two adult rove beetles (Staphylinidae), one probable leaf beetle (Chrysomelidae, Orsodacninae), and a spider; Cord. Cordoncillo female (ANSP 184707): arthropod fragments including at least two species of Hymenoptera (probably Ichnemonidae), several true weevils (Curculionidae), two fungus weevils (Anthribidae), one small beetle larva, two spiders, and a true bug (Hemiptera).

Relationships.—We are reluctant to suggest systematic relationships of *G. lineifrons* with other *Grallariculas,* because *lineifrons*' plumage and elevational distribution are unique, and the song is not known for *G. peruviana* and *G. ochraceifrons.* Now that tissue samples are available for almost all the taxa, applying biochemical techniques might resolve the relationships in this enigmatic group.

Acknowledgments.—The ANSP/MECN Ecuadorian program has been funded since 1990 by the MacArthur Foundation, and Krabbe's work was supported by the B. Benzon Fund. We thank Ing. Miguel Moreno of the Museo Ecuatoriano de Ciencias Naturales, Quito, for facilitating our work in Ecuador. The Ministerio de Agricultura, especially Sergio Figueroa, kindly provided authorization for our work. We are grateful to Jon Gelhaus and Tony Ruggieri of the ANSP Entomology Department for identification of stomach contents and to Bret Whitney for sharing his observations.

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Common Grackle predation on adult passerines.—Most published accounts of Common Grackles (*Quiscalus quiscula*) killing small songbirds (Townsend 1920, Christofferson 1927, Forbush 1927, Davis 1944, Bent 1958) are of birds that were recently fledged or were in a weakened condition. The following observations may be the first documentation of predation by a Common Grackle on several species of small birds.

From 1 May to 5 June 1992, I visited First Canadian Place Parkette in Toronto, Canada, on 31 days as part of a migration monitoring project. I made up to four visits per day and spent 80 h in total at the parkette which, during spring and fall migration periods, is a resting and feeding place for small passerines, the composition varying from day to day. The park is small (36 × 30 m) and is surrounded by high-rise office towers. About half the area is paved, and the remainder is lawn with plantings of birch and maple trees and several species of shrubs. An artificial waterfall is built into the building that borders the park on the north side.

I first saw a Common Grackle with an aluminum band on its left leg in the park at noon on 11 May; I last saw it on 1 June. In the intervening period, it appeared that the grackle killed and ate a total of 39 small passerines. I observed 12 of the kills and found the remains of 27 other fresh kills. The birds taken were Ruby-crowned Kinglet (*Regulus calendula*) 1, Ovenbird (*Seiurus aurocapillus*) 2, White-throated Sparrow (*Zonotrichia albicollis*) 35, and House Sparrow (*Passer domesticus*) 1.

Within an hour of its first appearance at mid-day on 11 May at 13:00 EDT, the banded grackle killed and fed on a White-throated Sparrow; at 14:00 it chased another which escaped. At 16:00 the grackle killed a second White-throated Sparrow and ate it; a few minutes later it tried to catch another, unsuccessfully. Twenty-four of the kills occurred in the first three days that the grackle was present. The last known kill (which was observed) was on 22 May. The reason for no further killings may have been lack of prey after the few surviving small, ground-frequenting species had fled the park. No White-throated Sparrows were seen in the park after 22 May. Although unsuccessful attacks were made the morning of 13 May on a Hermit Thrush (*Catharus guttatus*), a Wood Thrush (*Hylocichla mustelina*), and a Black-throated Blue Warbler (*Dendroica caerulescens*), no attacks were seen on other species in the park that included a variety of tree-frequenting warblers, Mourning Doves (*Zenaida macroura*), and a Brown Thrasher (*Toxostoma rufum*).

I observed a change in the grackle's method of hunting after the first two days. Initially, the grackle watched for its prey from a tree top perch from which it would attack any birds seen below. During the first two days it lost prey when it diverted its attention from one bird to another or drove birds upwards into the trees. By noon on 13 May (within 48 h), it had learned to target a specific bird and chase it down to the ground where it caught and killed it. From that time on, every chase seen ended in a kill. After a few days, the birds visiting the park became aware of the danger. When the grackle appeared the birds gave warning calls, took cover, and ceased all singing and movement. Then, the grackle again adjusted its method of hunting. It began to use hidden lookouts. It watched from building ledges above the trees where it could see into the trees easily but could probably not be seen by the birds in the park. It also began methodical explorations of the trees, usually flushing one or two birds out of hiding.

Many of the birds were caught on the paved walkways and carried in the grackle's claws (if still alive) or in its bill (if dead) into the shrubbery for feeding. They were eaten immediately, except for 12 May when three kills found intact in the early morning were eaten later the same day. Three spots in the shrubbery were favored for feeding, and the remains of from five to nine dead birds were clustered in these areas. After feeding on the latest kill,

the grackle would also return to feed on previous kills. The grackle always started feeding by placing the victim flat on its back, plucking out the breast feathers, and eating the breast first. Usually the remainder was eaten on one of its return visits. On two occasions, it was starting to feed on birds whose wings and tails were still fluttering. The grackle preferred its prey to other food. When I covered dead birds with raw hot dog and hamburger meat, the grackle pulled the prey from under them and moved elsewhere for feeding, leaving the proffered meat uneaten.

No more than two grackles were seen at the park until 3 June when, at 11:14, three grackles landed on the centre lawn and foraged in the grass for 8–10 min. The largest wore a band on the right leg that appeared thicker and chunkier than the one on the killer's left leg. These and others appeared during June, but the banded killer grackle was not seen again.

The success of the grackle's predation resulted from its ability to take advantage of the artificial situation set up by this small island of plantings surrounded by high buildings. The prey birds were concentrated into a constricted area from which escape was difficult, and they may have been weakened by migration.

Acknowledgments.—This study was part of a cooperative study by the Toronto Ornithological Club involving the monitoring of Neotropical migrants through Metropolitan Toronto. I thank George M. Fairfield for commenting on earlier versions of the manuscript.

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ORNITHOLOGICAL LITERATURE

BIRD CENSUS TECHNIQUES. By Colin J. Bibby, Neil D. Burgess, and David A. Hill. Academic Press, London, San Diego. 1992:257 pp., 116 boxed figures with commentary, 1 table. $39.95.—The purpose of this book is to familiarize the researcher with the commonly used methods for estimating relative abundance and trends in the size of bird populations and to warn users of the biases in each method. This is not an exhaustive review of bird-census literature but features specific examples to illustrate the methodologies, options, biases, and pitfalls. Although the introductory paragraph refers to two important American publications on bird-census methodology (Ralph and Scott 1981, Stud. Avian Biol. 6; Verner 1985, Current Ornithology 2:247–302), the book principally addresses a British audience; the most recent American references are from 1989. Most of the abundant examples in the boxed annotated illustrations are from the British literature, and the reference list includes only two foreign-language titles.

After an introductory chapter on purpose and design in counting birds and an eight-page table with examples of the uses of each major census method, there are separate chapters on census errors, territory mapping, transects, point counts, banding, individual species, colonial and flocking birds, distribution (atlas) of birds, and habitat description. Each chapter concludes with a helpful summary and list of points to be considered.

I encountered a problem in the first boxed illustration. Here the authors assume that the reader knows how to locate square 02 on a hypothetical county map of magpie distribution; not even the British breeding bird atlas (Sharrock 1976) described the peculiar vertical sequence in numbering the British atlas blocks. American readers will search the index in vain for references to the Breeding Bird Census, the MAPS program, migration sampling and winter studies. Reference to the "remarkably ill-standardised Christmas Bird Count" centers around Root's (1988) winter atlas, which is the only U.S. atlas mentioned in the book. "CBC" refers to the British Common Birds Census, not the Christmas Bird Count.

Emphasis is on helping the reader make sound selections of methodology for specific studies, avoid pitfalls, and recognize limitations on interpretation of the results. For the most part, the illustrations are well chosen for emphasizing the authors' points. One might profitably spend an hour or two just studying the boxed examples for an overview of the many problems in bird censusing.

Territory mapping is the only bird-survey method for which the methodology is internationally standardized (International Bird Census Committee 1969, 1970), and it has long been considered the standard against which other methods are judged. The authors believe this view is unjustified because some species are not strictly territorial. Mapping is unsatisfactory for semi-colonial, colonial, and wide-ranging species and for species with very brief song periods. The mapping method is also the most time-consuming. In spite of these criticisms, the authors do not recommend any other method as the standard. In fact, they mention the value of the mapping method if bird populations are to be related to habitats. I especially appreciate the emphasis on recording simultaneous registrations of birds, a feature of mapping censuses that is overlooked by many writers.

The authors consider transects particularly suitable in extensive, open, uniform, or species-poor habitats, and state that, where their use is appropriate, they can be less time consuming than point counts. The use of transects may also be more accurate because errors in distance estimation accumulate linearly in transects but by squares in point counts. For habitat correlations, however, mapping censuses or point counts are preferred. A procedure not found in American publications is the Look-see method, which can be used for species such

as the Barn Owl in special situations where nesting sites are so few and obvious that essentially each is found and examined.

The chapter on banding focuses on estimating population size with the Lincoln (1930) index and the du Feu (1983) method. The latter procedure (Ringing and Migration 4:211–226) uses multiple captures during a single mark-recapture session. Unfortunately, the more sophisticated recent literature on analyzing mark-recapture data is not mentioned. Anyone attempting such a study would be well advised to read the three pages of assumptions that should not be violated.

The species index is not user friendly. It is arranged taxonomically by English names of either order (passerines) or family or subfamily (terns), under which one searches alphabetically for the species name. For example, Kestrel, European, *Falco tinnunculus,* is found between Hen Harrier, *Circus cyaneus,* and Marsh Harrier, *Circus aeriuginosus* (sic.), under the heading "Birds of Prey." One might quibble over the misspelling of scientific names in the species index or the misciting of the Christmas Bird Count circle radius as 15 instead of 7.5 miles, but mistakes are relatively few.

The attractive volume is sturdily bound. A male Fuerteventura Stonechat (*Saxicola dacotiae*), a Canary Island endemic, graces the front cover. I recommend this book to anyone interested in studies of bird populations. It gives an excellent review of methods, especially those that are applicable during the breeding season when populations are relatively static. Although some of the methods and especially potential sources of error apply also to the winter and migration seasons, the authors' main emphasis is on the nesting period. Depending on the study to be conducted, American references also should be consulted, particularly Ralph and Scott (1981), Verner (1985), Handbook for Atlasing American Breeding Birds (Smith 1990, Vermont Inst. Nat. Sci., Woodstock), Inventory and Monitoring of Wildlife Habitat (Cooperrider et al. 1986, U.S. Dept. Inter., Bur. Land Manage., Denver), Modeling survival and testing hypotheses using marked animals (Lebreton et al. 1992, Ecol. Monogr. 62:67–118), and the references cited by Lowe (1993, J. Field Ornithol. 64 suppl.: 3–4).—Chandler S. Robbins.

The Private Life of James Bond. By David R. Contosta. Sutter House, Lititz, Pennsylvania. 1993:127 pp., color frontispiece (childhood portrait), photographs. $16.95.—I think it is safe to say that no ornithologist who was not also an artist has been featured in as many biographical publications as the late James Bond (1900–1989). As the long-established authority on the birds of the West Indies, his scientific career was covered in obituaries in ornithological journals (Parkes, 1989. Auk 106:718–720; Snow, 1990. Ibis 132:130). As for other aspects of his long life, these were chronicled in a series of books by his wife, Mary Wickham Porcher Lewis Bond, already an established writer by the time of their marriage (her second, his first) in 1953.

The latest addition to Bondiana is a slim volume by David R. Contosta, Chairman of the History Department at Chestnut Hill College, Philadelphia, and a family friend of the Bonds. His previous books have dealt mostly with biography and with aspects of the history of the Philadelphia suburbs; Mrs. Bond, who cooperated closely with Mr. Contosta, believed that Contosta's interests made him an ideal author for an account of James Bond's life that would touch only peripherally on his ornithological achievements.

There is, of course, much overlap with the material in Mrs. Bond's books: "How 007 Got His Name" (1966); "Far Afield in the Caribbean" (1971); "To James Bond With Love" (1980); "Ninety Years 'At Home' in Philadelphia" (1988). As befits a book by a historian/

biographer, the two chapters covering Bond's antecedents and his life before his marriage to Mary are more thorough than in her books, and include a generous number of photographs (the equivalent period of Mary's life is covered in "Ninety Years").

Contosta's text is quite readable, although as a historian his style is understandably less lively than that of Mary Bond. The sources of his information and his quotations are thoroughly footnoted. The book will be useful for scholars of the history of American ornithology, and for anyone curious about the life of one of the last of the great ornithologists who made a permanent impact on our discipline in spite of never achieving an advanced degree.—Kenneth C. Parkes.

Threatened Birds of the Americas. The ICBP/IUCN Red Data Book. Third Edition Part 2. By N. J. Collar, L. P. Gonzaga, N. Krabbe, A. Madroño Nieto, L. G. Naranjo, T. A. Parker III, and D. C. Wege. Smithsonian Institution Press, Washington, in Cooperation with the International Council for Bird Preservation. 1992:1150 pp. $75.—The long-awaited Red Data book for the western hemisphere makes a timely arrival with this impressive compilation. The title is somewhat misleading since after treating the 302 forms from South and Central America and the Caribbean Islands, it became necessary to defer the 25 North American and the "Neotropical Pacific" species to a future volume. An appendix gives a brief treatment of these species.

Forty-eight families are represented in the listing. As might have been expected the family Psittacidae with 38 species treated has the most threatened forms. The Trochilidae and Formicariidae with 28 each follow. Some of the species included should probably be considered to be subspecies of other forms, but the authors have wisely decided to treat them as distinct forms. As might be expected many of these forms are poorly known, often from only a few specimens collected years ago.

The species are classified in a 12-point scale, with five categories of Endangered, three categories of Indeterminant, for which insufficient information is available, and four categories of Vulnerable or Rare. There are 96 species listed as "Endangered" of which 23 species are listed as "Endangered/Extinct, Situation Terminal." for which action is urgent if population is indeed extant. This list includes the Ivory-billed Woodpecker (*Campephilus principalis*), the Eskimo Curlew (*Numenius borealis*), and Bachman's Warbler (*Vermivora bachmani*). Five species are listed as "Situation unclear urgent if taxonomic status confirmed". Seven species are listed as "perhaps in need if and when found" and 31 species are considered "insufficiently known." However, the picture is not totally gloomy, as occasionally a species account details the rediscovery of a species, not otherwise reported for years.

The species accounts follow a set pattern, leading off with a brief summary statement on the status. A section on Distribution discusses in detail the specimen records as well as other published records. The sections on Population and Ecology give what is known for the species, which in many cases is very little. These are followed by sections entitled "Threats," "Measures Taken," and "Measures Proposed." The threats almost always are the loss of habitat, either by clearing of the forest (not always primary forest) or drainage of wetlands. Measures taken or proposed usually involve the preservation of the habitats, as for example in the establishment of a reserve. In many cases the only measure proposed is for further research. For many species, so little is known that assigning a threat cannot be done. A section on Remarks includes taxonomic history or other pertinent material. It would appear that these accounts are essentially complete and include everything that was known about the species at the time of writing. Several appendices organize this massive data set in useful

ways. The species in each of the categories are listed, a tabulation by country is given (Brazil leads the list with 97 entries), and a list of 325 additional "Near-threatened" species is given. This comprehensive survey may have arrived too late to help many of its subjects, but it does provide guidance for some conservation efforts.—George A. Hall.

Florida Bird Species. An Annotated List. By William B. Robertson, Jr., and Glen E. Woolfenden. Spec. Publ. No. 6, Florida Ornithological Society, Gainesville, Florida. 1992: 260 pp., 1 fig., 1 table, and 3 appendices. Cloth $22.95, Paper $17.95 (plus $2.00 per book shipping, Florida residents add 7% sales tax); Available from Florida Ornithological Society, Archbold Biological Station, P. O. Box 2057, Lake Placid, Florida 33852.—When the Florida Ornithological Society was founded in 1972, one of its early goals was to publish an annotated list of Florida birds. Forty years earlier Howell's (1932) Florida Birdlife had appeared (updated by A. Sprunt in 1954), and although Henry Stevenson was working on a new comprehensive text (Stevenson and Anderson, in press), it was felt that an annotated checklist would be helpful to the many birders—both residents and visitors—in Florida. A committee was appointed, museum research conducted, and drafts circulated. In the late eighties Robertson and Woolfenden grabbed the floundering bull by the horns and the result is this outstanding publication.

It is an annotated list of all bird species reported to have occurred in Florida through 31 December 1991. Included is a list of 461 verified species (a specimen, photograph, or voice recording of unquestioned provenance) and three appendices: A—Unverified stragglers (75 species), B—Probably unestablished exotics (16 species), and C—Unestablished exotics (119 species).

Florida's geographical position on the Atlantic and Gulf of Mexico, with the southern part of the peninsula extending into subtropical waters, results in a number of western, northern, and Caribbean stragglers in the state. Miami is a major port for the avian pet trade, and with a large Hispanic population, many of whom keep caged birds, it is no surprise that so many exotic species have escaped or been released. The mild climate and the abundant exotic flowering and fruit-bearing trees and shrubs planted as ornamentals, in addition to back yard feeders, provides the sustenance for longterm survival of many individuals of these species.

Several pages of the Introduction are devoted to comments on the changes in bird populations during the 20th century, especially the latter half. Howell (1932) reported 361 Florida species, Sprunt (1954 and a 1964 addenda) reported 411 species, Stevenson (1976) 463 species, and the current list (1992) now totals 536 species. About 65 species have expanded their breeding ranges in Florida, chiefly species closely associated with altered habitats. In contrast, about 30 species show a receding breeding range, apparently unable to adapt to altered habitats. Most of these are colonial wading birds or species associated with pineland, prairie, and scrub habitats.

The following information is presented for each species: Evidence of occurrence, distribution in Florida, the salient characteristics (seasonality, abundance, frequency, habitat, life history context) of its occurrence, and how, if at all, has its pattern of occurrence changed during the period of record.

Appendix A is a catch-all category ranging from species that have been seen over and over again (for example, Red-necked Grebe [*Podiceps grisagena*] and Rough-legged Hawk [*Buteo lagopus*]) but for which no verifiable evidence (specimen, photo, etc.) exists, to species mentioned in print in the 18th and 19th centuries based on observation only, or specimens

now lost or of dubious origin. All such reports were included so that they would be available for re-evaluation rather than to be arbitrarily deleted and lost. Appendix B lists those exotic species that breed regularly (or once did) in Florida, but do not yet appear to have a self-sustaining wild population. Appendix C lists those exotics that have been seen in the wild, some may have bred, but for the most part they are not self-sustaining populations at this time. Needless to say, this is the most incomplete list in the book.

The authors hope that the emphasis placed on verifiable evidence and published accounts will stimulate Florida birders of all degree to seek and preserve the best possible supporting documentation and to publish their important observations. Hereafter, birders will turn to Florida Bird Species as their initial reference to learn the significance of an observation.—Herbert W. Kale II.

Atlas of Breeding Birds in Pennsylvania. Edited by Daniel W. Brauning. Univ. Pittsburgh Press, Pittsburgh. 1992:484 pp., 8 acetate overlays. $29.95.—Breeding bird atlases have become one of the more important results produced by the non-professional birding community. They provide a wealth of distributional information for our breeding avifauna, serving as a benchmark against which future range and status changes can be compared.

The contents of the Pennsylvania atlas are similar to other breeding bird atlases that have been published previously. The four introductory chapters describe the atlas methodology employed in Pennsylvania, a brief summarization of the results, a description of climatic and physiographic features of the state, and a brief history of Pennsylvania ornithology. Most of the book is devoted to the species accounts written by 21 authors. The content of these accounts vary from species to species, but are largely devoted to discussions of the atlas results and historic changes in status and distribution. Maps depicting the atlas records, tables summarizing these data, and a black and white line drawing are provided for each species. Data from the North American Breeding Bird Survey (BBS) is depicted graphically for those species adequately surveyed in Pennsylvania. Among the appendices are brief accounts of the 16 species that have nested in the state but were not encountered during the atlas, and a large table summarizing egg and fledgling dates for Pennsylvania.

The 2050 participants embarked on the ambitious goal of atlasing every one of the 4928 blocks within the sate. They succeeded in adequately covering many of these blocks, but there were areas where the coverage was less rigorous. These coverage problems generally are not apparent in the distribution maps, however, which correspond well with similar maps produced by breeding bird atlases in the surrounding states. The treatment of BBS data should be viewed with some caution. The discussion of BBS population trends in the text is based on the results of the route-regression analysis routinely performed by the U.S. Fish and Wildlife Service (USFWS). The graphic presentation of the BBS data represent annual changes in the mean number of birds per route, which may or may not directly correspond with the trends calculated by the USFWS. Where discrepancies occur, the route-regression results are more reliable.

This book provides a wealth of information on the historic and current distribution of Pennsylvania's breeding birds. As the culmination of countless hours of field work over a seven-year period, everyone who participated in the data collection and preparation of the manuscript should be proud of their efforts. Anyone with an interest in this diverse avifauna will find the atlas to be a valuable source of timely distributional information.—Bruce G. Peterjohn.

MANUAL OF ORNITHOLOGY. AVIAN STRUCTURE AND FUNCTION. By Noble S. Proctor and Patrick J. Lynch. Foreword by Roger Tory Peterson. Yale University Press, New Haven. 1993:340 pp., many black-and-white drawings and photographs. $40.00.—At first glance this book makes a favorable impression because of the attractive drawings, but a closer inspection reveals some serious problems. It is meant to serve primarily as a laboratory guide for a course in ornithology, and secondarily as a reference manual. With one chapter on systematics, one on field techniques, and nine on the organ systems, this is mainly a treatise on avian structure. It is difficult, however, to understand how it is meant to be used in the classroom because there are no specific dissection instructions. Indeed, in his Foreword to the book, Roger Tory Peterson states "As we slowly evolve from the age of dissection, here is a book that will help us to understand the internal structuring of birds without the need to dissect them in the laboratory." This is about as realistic as thinking that we can learn to identify birds just by looking at the pictures in a field guide.

The chapter on systematics has a number of misinterpretations. With respect to higher-level relationships it gives the impression that the field consists of only two parts; morphological systematics as practiced by Gadow, and biochemical systematics as practiced by Sibley and Ahlquist. Morphological characters that vary little are "conservative" and are somehow thought to contain phylogenetic information, while characters that change in relation to behavioral evolution are "plastic" and therefore less useful. This inverted notion seems to suggest that adaptive evolution is more likely to reflect convergence than common ancestry, but no explanation is offered. There is no hint that morphological methods have changed in the last 100 years, or that the character concept is no longer exemplified by palate types or muscle formulas. Cladistic analysis is not explained, nor is the interdependency of morphology and biochemistry through congruence testing of phylogenetic hypotheses.

Convergence is defined as a situation where "completely unrelated" groups evolve similar traits. What is meant, of course, is that similar traits evolve independently in groups whose last common ancestors lacked those traits. This is not just semantic carelessness; the use of "unrelated" reveals a failure to understand that classification today is based on phylogeny, which is a pattern of relationships of common descent.

Another example of the confusion engendered by a failure to distinguish between classification and phylogeny is provided by the discussion of divergence. Referring to the Order Ciconiiformes of Sibley and Ahlquist, which includes storks, New World vultures, penguins, birds of prey, loons, etc., Proctor and Lynch suggest that "the new Order Ciconiiformes is surely the best example of divergent evolution ever devised." How could this be? Any clade larger than, but including the Ciconiiformes will show more divergence. I suspect that the problem arises from a supposition of categorical equivalence between orders in different classifications.

The discussion of subspecies is also flawed. Subspecies are defined as geographic variants that are distinguished from the parent species, rather than from other subgroups of the parent species. "Thus the pale Song Sparrows . . . are called *Melospiza melodia saltonis,* to distinguish that form from the parent species" (p. 34). Actually that form *is* part of the parent species, and is being distinguished from other subspecies.

The chapters on the organ systems of birds are flawed by a recurring set of problems: (1) Different terms are used for the same structures in text and figures. For example, in the text the premaxilla is said to have *nasal, dentary,* and *palatal* processes, but in the figures it is labelled with *nasal, frontal,* and *maxillary* processes. Similarly, on p. 131 the text refers to the *spinous process* of a vertebra, but the accompanying illustration calls it the *neural spine.* (2) The selection of structures to be named is arbitrary. On p. 129 a ventral view of the

skull shows many nerve foramina, but only the hypoglossal foramen is identified. Of what use is such incomplete information? (3) Some labelled structures are not discussed, and some structures are discussed but not labelled; (4) There are errors. On p. 119 the first *phalanx* of digit IV is mislabelled *metatarsals.* The gastrocnemius muscle does not "flex the digits of the foot", nor do Mm. flexor perforans et perforatus II and III insert on the *dorsal* surface of the phalanges (p. 164). The figure on p. 165 shows a muscle whose belly is labelled *Flexor perforans et perforatus iii,* but whose tendon is identified as *Flexor digitorum longus.* Problems like these are sufficiently numerous to seriously compromise the utility of the book.

Another shortcoming is poor editing. Singular and plural usages are confused and nouns are used as adjectives. For instance, on p. 140 we read that "The pelvis has two openings, or foramen." One of these lies "posterior to the acetabulum joint . . ."

Finally, the terminology employed for anatomical structures is a mixture derived from various sources that do not always represent the most recent work: a standard nomenclature for avian anatomy has been available for over a decade and should be used in works of this kind (Baumel, J. J., A. S. King, A. M. Lucas, J. E. Breazile, and H. E. Evans. 1979. Nomina Anatomica Avium. Academic Press, London).

Scattered through the book are boxes whose illustrations and text make specific points about avian biology, and many of them are accurate and interesting. But again there are difficulties. On p. 35, for example, a discussion of subspecies in the Song Sparrow (*Melospiza melodia*) states that there is "a well-known cline in body size." The drawing, however, depicts the different subspecies as being of equal size.

The illustrations are the best part of this book and it is unfortunate that the text does not achieve the same standard of excellence. As a laboratory manual, Proctor and Lynch competes with an established standard (Pettingill, O. S., Jr. 1985. Ornithology in Laboratory and Field. Fifth edition. Academic Press, Orlando). The illustrations are superior to those in the latter work, but as for information content and class exercises it is no contest. If I were choosing books for class use I would provide a copy of Proctor and Lynch as a reference, but would use Pettingill as the laboratory manual.—Robert J. Raikow.

Bird Anatomy II. The Surface Anatomy of Birds. By Patrick J. Lynch and Noble S. Proctor. Yale University Press, New Haven. 1993. Four 800K disks, plus User's Guide. $75.00.—This computer program is intended to supplement the authors' book, "Manual of ornithology. Avian structure and function" (Yale University Press, 1993). It contains a series of lessons on general anatomy, skeleton, head, wings, flight, and feathers, with a little on muscles and almost nothing on visceral systems. The technical requirements for running this software are a Macintosh computer with operating system version 6.07 or later, 2 megabytes or more of RAM, a hard disk with 2.5 megabytes or more of free space, and HyperCard version 2.1 or later.

Educators have heard many glowing predictions about computerized instructional materials, but those that I have seen have been disappointing, and this one is no exception. The supposed advantages of such a program over a book include animation, sound, and multiple pathways through the information. Animation in the present program is rare and rudimentary: air moves through a diagram of the respiratory system, two muscles laboriously raise and lower a humerus, and from time to time an otherwise immobile bird opens its bill and chirps. The latter is about the extent of sound production in this program. The use of alternate pathways is more successful here, and yet it is not clear that anything is achieved that could not have been accomplished by cross references and page-turning in a book.

Another computer trick involves the mouse. By clicking on the illustrations, one can make labels and text appear and disappear. Some of the problems in the implementation of this capability may be illustrated by the structure of the skull in lateral view. In the book there is a labelled drawing on p. 125. In the program the same drawing is reproduced, but takes two screens for the posterior and rostral regions. The drawings in the program have only some of the labels found in the book. To see the rest one must click on the structures, as though they had been removed in an effort to make the experience more interactive. Unfortunately the labels are not always the same in the two media. The *parietal* of the program is called the *squamosal region* in the book, while the *parietal region* of the book has become the *occipital* of the program. The *pterygoid* of the book has no name in the program. The *nasal process* of the *premaxilla* in the book is called the *frontal process* in the program. The frontal process of what? Clicking reveals that the *premaxilla* of the book has become the *maxilla* in the program. The same structure may even have different names within the program itself. The angle of the lower jaw is called the *articular* in one screen and the *angular* in the next. Perhaps it is a sense of embarrassment that causes the computer to frequently produce at this point an offer to let one quit.

This program has an optional feature that I did not experience. It may be used with a videodisc player and color monitor to run the videodisc *Encyclopedia of Animals, Volume 4, Birds 1,* which provides additional pictures on screen.

I cannot recommend Bird Anatomy II as a serious learning tool. Its information content is limited and inaccurate, and its interactive features are rudimentary. Read a good book.—Robert J. Raikow.

The Ostrich Communal Nesting System. By Brian C. R. Bertram. Monographs in Behavior and Ecology. Princeton Univ. Press, Princeton, New Jersey. 1992:196 pp. 46 black-and-white plates, 48 figs., 35 tables. $35.00.—This is a good reference for anyone interested in Ratites, mating systems, or ostriches in general. While the study was conducted on the Masai ostrich, (*Structhio camelus massaicus*), the information should apply to all ostriches.

The book begins with a chapter on the bird itself, along with information on the subspecies of ostrich, their distribution, habitat, feeding behavior and their relationship with man. The author then describes previous studies of ostrich along with a summary of ostrich behavior before explaining details of his study.

The next chapter on Methods describes the basic parameters of the study, with the following chapters, entitled "The Population" and "The Breeding System" going into the population and breeding biology of the species. These are followed by a chapter on the ecological relationships and aspects of the information provided in the prior chapters.

Chapters on the reproductive strategies of males and females lead right into the final discussion and comparisons with other ratites. The discussion includes comparisons to a variety of other social systems found in birds and as a result is a first rate review of social systems and strategies found in birds. The review of the literature in chapter nine and the list of references following it are extremely useful for anyone interested in the reproductive biology of ratites.

In the discussion section entitled "The Evolution and Maintenance of the Communal Nesting System" the author compares the system of ostriches to all other ratites—cassowary, emu, and rhea. This section provides a good review and is very useful to anyone interested in this group of birds. The ostrich is a unique bird, the largest living bird; it has a very interesting social system which shows a lot of similarities to other ratites but also some interesting differences. The fact that ostriches must have evolved with and have survived

in an environment with a vast assortment of large mammalian predators has probably influenced their social system and reproductive strategies significantly.

With the current great interest in breeding ostrich with the intent of developing a major ostrich industry in the United States and in other portions of the world, this book should prove useful to a variety of people. It can also be used to assist in the development of management techniques based on the natural social and reproductive systems of wild ostriches. As a result, everyone ranging from the biologist interested in social systems and strategies to the potential ostrich rancher should find this book to be as interesting and useful as I did. I certainly recommend the book highly for these reasons.—Donald Bruning.

Roberts' Birds of Southern Africa, Sixth edition. By Gordon Lindsay Maclean, illus. by Kenneth Newman and Geoff Lockwood. The Trustees of the John Voelcker Bird Book Fund, Cape Town, South Africa. 1993. ixxx & 871 pp., 3 maps, 77 color plates. No price given.—"Roberts" is the standard handbook for birds of southern Africa, and the sixth edition is an update of the 1985 edition. It gives current and comprehensive accounts for birds in Africa south of Angola and the Zambezi River. The text is modified slightly in about 60% of the species accounts, and 16 species were added to the southern African list, most of them vagrants. The color plates are attractive and adequate for identifying birds in the field.

The introduction is a text on systematics, names, topography, song, habitats, a glossary of ornithological and zoological terms, a list of general and historical readings, and maps of localities, rainfall, and habitats. A new feature is a set of keys to certain groups. The characters used are mainly plumage and bill traits that are visible in the field. The keys may be useful for the nightjars and larks if the birds are in the hand. References are given for many birds in the species accounts.

As in the fifth edition, audiospectrograms of songs are included. This is a useful feature. In Zimbabwe, I was able to identify a small rail as a Streaky-breasted Flufftail (*Sarothrura boehmi*) from a glance of a bird and a recording of its call by checking the descriptions and audiospectrograms in the fifth edition. In the sixth edition, the sound traces are blurred and the lettering is less legible for those songs that are in both editions. The choice of songs is a mixed lot and in some cases the songs are not diagnostic of the species. The brood-parasitic *Vidua* finches, which mimic the songs of their foster species, are represented in some song diagrams by their nonmimetic songs (in the paradise whydahs *V. paradisaea* and *V. obtusa*), and the mimicry songs shown are not similar to the foster species' song models in some others (in the indigobird *V. chalybeata*). Including the nonmimetic songs is not helpful for these species, even though these were the songs most readily available on the commercial recordings from which the audiospectrograms were taken.

The species included are generally up to date. Some questionable birds are included. The record of a "violet widowfinch" is based on an unidentified female seen in 1973 near a "Brown Firefinch" (*Lagonosticta* (*rufopicta*) *nitidula*) on an island in the Zambezi, and not on song mimicry or on a morphologically distinct male. This record appears much as in the fifth edition, but the species name here is different, reflecting the observation that the supposed species has the same song mimicry of Bar-breasted Firefinch (*Lagonosticta rufopicta*) as in Wilson's Indigobird (*V. wilsoni*) in West Africa, as noted in the review of the fifth edition. The color plate of this bird is imaginative. On the other hand, the sixth edition was produced too early to include a recently recognized distinct species, the Green Widow-

finch or Indigobird *Vidua codringtoni,* which mimics and is associated with Peters' ("Red-throated") Twinspot *Hypargos niveoguttatus* (*Ostrich* 63:86–97, 1992).

The sixth edition of Roberts' is an informative and attractive handbook, and I recommend it to all persons and institutions with an interest in the birds of Africa—ROBERT B. PAYNE.

ECOLOGY AND MANAGEMENT OF THE MOURNING DOVE. A Wildlife Management Institute book compiled and edited by Thomas S. Baskett, Mark W. Sayre, Roy E. Tomlinson, and Ralph E. Mirarchi. Technical editor Richard E. McCabe. 1993. Stackpole Books, Harrisburg, Pennsylvania. 567 pp. $44.95.—The Mourning Dove (*Zenaida macroura*) is the most abundant and the most widely-distributed gamebird in North America. As a result of these characteristics and its desirable sporting qualities, it is harvested in larger numbers than is any other North American gamebird. Although classified as a gamebird in most states, Mourning Doves are classified as songbirds in at least seven states. The adaptability of Mourning Doves to residential areas where they nest and frequent bird feeders has resulted in their increased popularity as a songbird. In most states they play a dual role of gamebird and songbird. Their pleasing vocalization, quiet demeanor, physical attractiveness, and acrobatic aerial skills have made them favorites of both amateur and professional ornithologists. In spite of, or perhaps because of, these attributes no comprehensive books have ever been written about the Mourning Dove. This book is not only the most comprehensive ever written about Mourning Doves, but one of the most comprehensive ever written about any bird.

A total of 29 chapters are included in four sections: (1) Introducing The Mourning Dove, (2) Life History and Biology, (3) Population Characteristics and Harvest, and (4) Research and Management. Chapters are authored by 24 different authorities and nearly 200 persons were involved in reviewing the final manuscript.

The book is not only informative to read, with 99 tables and 73 figures, but enjoyable to examine because of the nearly 400 photographs and the interesting illustrations of Harold Irby and Francis Sweet. Scientists involved with research or management of Mourning Doves will benefit from this book as a result of the compilation of scientific data covering all aspects of Mourning Dove biology. Amateur ornithologists will appreciate the in-depth life history information which has never before appeared in one publication.

The overall quality of "Ecology and Management of the Mourning Dove" is excellent. Typographic and scientific errors appear to be nonexistent, as one would expect from a book written by specialists, edited by professionals, and published by Stackpole Books. The index is thorough and enables readers to locate almost any subject of interest. Over 1400 references add to the value of the book and most likely include every important publication dealing with Mourning Doves.

Future habitat and harvest management of Mourning Doves will be improved as a result of this book, because area wildlife managers can better relate the temporal and geographic relevance of their actions to the dynamics of the total Mourning Dove population in their management unit. This book will undoubtedly result in the improved quality of future research design and direction. Research priorities for all aspects of Mourning Dove management are discussed in the final chapter. The authors state, "In our view, the two most important issues for Mourning Dove managers today are (1) population declines throughout the Western Management Unit (WMU) and in the eastern tier of the Central Management Unit (CMU), and (2) the lack of a standardized nationwide harvest survey." The authors also describe research needs for: (1) assessment of breeding population status, (2) assessment

of mortality, (3) assessment of productivity, (4) relationships with habitat, (5) biology, and (6) harvest management.

Although the overall value of this publication is quickly evident to any reader, one of its greatest contributions will be the standards it sets for similar books written on others species in the future.—Edwin D. Michael.

Erratum

In "Migration of woodland birds at a fragmented inland stopover site" by Kevin Winker, Dwain W. Warner, and A. R. Weisbrod (Wilson Bull. 104:580–598), the statistical results in Table 3 (p. 591) were not presented correctly. In the first two rows of the table, the lines denoting statistically different groups should be broken three more times. These breaks should appear between Swamp and Floodplain in both of the first two rows, and between Floodplain and Willow in the second. The groupings for the first two rows are thus: Spring: (Swamp) (Floodplain, Willow) (Willow, Upland), and Autumn: (Swamp) (Floodplain) (Willow, Upland). The lower half of the table is correct.

In addition, two confusing lines appear in the text. The first sentence in the second full paragraph on page 582 should read "Our netting periods spanned the bulk of both spring and autumn migration (Fig. 1), but did not encompass the full migratory period of several species, most of which were Nearctic-Nearctic migrants (unpubl.)." The third sentence in the only complete paragraph on page 593 should read "For ground-foraging species this is not a problem, but most of the species captured at our site forage above ground or near-ground levels."

Wilson Bull., 106(1), 1994, pp. 187–188

INFORMATION FOR AUTHORS

The Wilson Bulletin publishes significant research and review articles in the field of ornithology. Mss are accepted for review with the understanding that the same or similar work has not been and will not be published nor is presently submitted elsewhere, that all persons listed as authors have given their approval for submission of the ms, and that any person cited as a personal communication has approved such citation. All mss should be submitted directly to the Editor.

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The editor welcomes queries concerning style and format during your preparation of mss for submission to the *Bulletin.*—Charles R. Blem, Editor.

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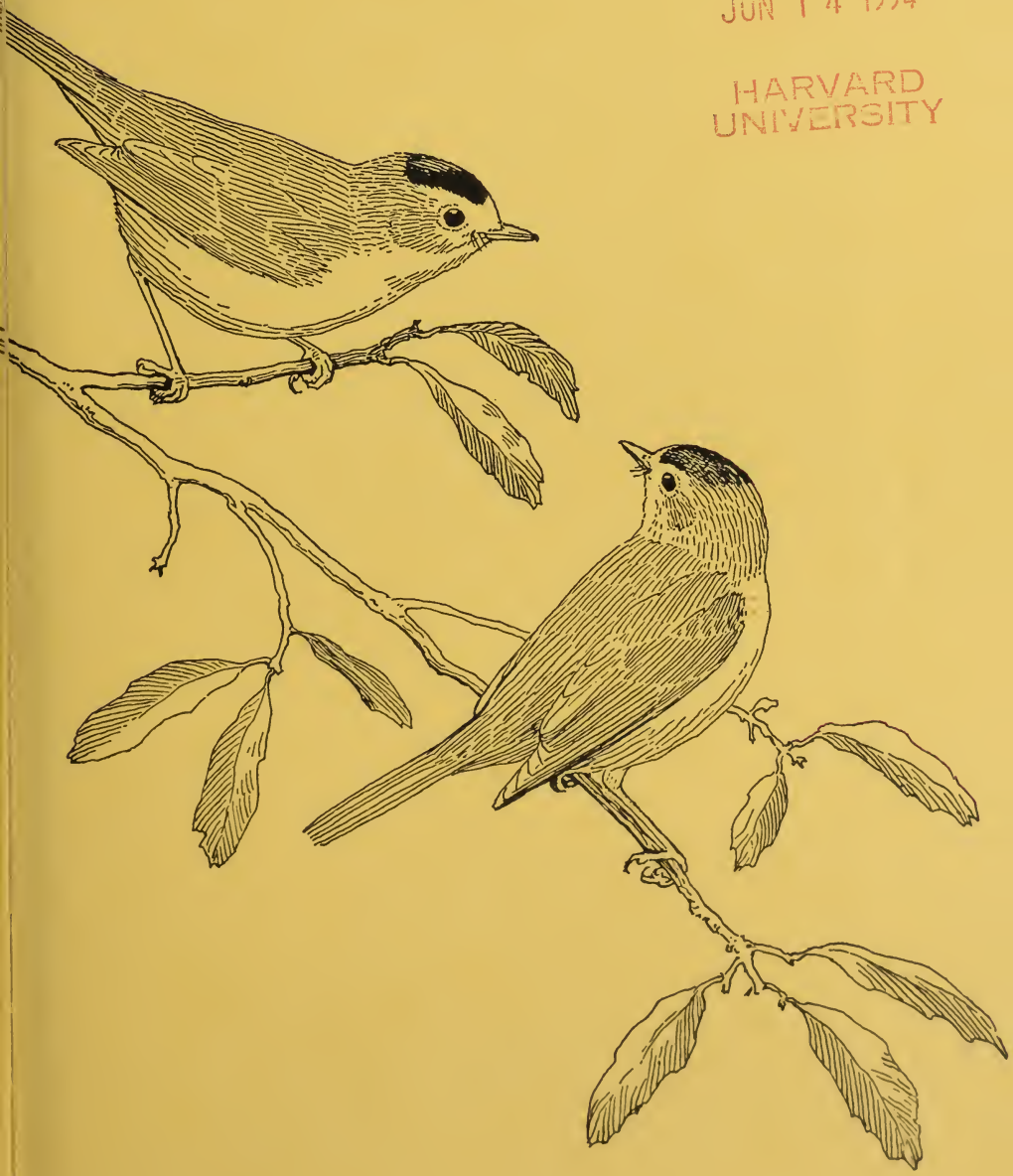

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Hybrid White-throated Sparrow × Dark-eyed Junco (*Zonotrichia albicollis* × *Junco hyemalis*). Original painting by John C. Anderton.

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BEHAVIOR AND PARENTAGE OF A WHITE-THROATED SPARROW × DARK-EYED JUNCO HYBRID

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ABSTRACT.—A hybrid White-throated Sparrow (*Zonotrichia albicollis*) × Dark-eyed Junco (*Junco hyemalis*) was captured in Oct. 1991 in Potomac, Maryland, and studied in captivity until July 1992. The hybrid sang a mixed song composed of a junco trill followed by sparrow "peabody" notes. Another song included 30 notes, with only two recognizable as sparrow and six as junco notes. The hybrid responded most actively to playbacks of its own song, similarly to songs of a junco and a sparrow, and least to a Wood Thrush (*Hylocichla mustelina*) song. When the hybrid was presented with same-sex, sparrow-junco pairs, the hybrid showed no difference in behavior toward the males, but spent significantly more time, and flew, hopped, called, and preened more on the side with the female sparrows than with the female juncos. Based on mitochondrial DNA analysis, the hybrid's mother was a White-throated Sparrow. *Received 3 Sept. 1992, accepted 15 Sept. 1993.*

Roughly ten percent of all bird species are known to hybridize (Grant and Grant 1992). In this paper, we describe vocalizations and other behaviors and present mitochondrial DNA (mtDNA) evidence for maternal identity of a hybrid White-throated Sparrow × Dark-eyed Junco (*Zonotrichia albicollis* × *Junco hyemalis*) captured in Potomac, Maryland. This is the fourteenth such hybrid presented in the literature (Eastman and Eastman 1966, Blem 1981 and refs. therein, American Birds 1992), and the first to be studied in captivity.

METHODS

On 25 Oct. 1991, a White-throated Sparrow × Dark-eyed Junco hybrid adult male (sexed by gonads post-mortem) was captured by Margaret T. Donnald in Potomac, Maryland

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(Montgomery Co.) at the Adventure Bird Banding Station (see Donald and Maane 1992 for description of plumage and morphology). The hybrid was transported to the Dept. of Zoological Research at the National Zoological Park in Washington, D. C., and placed in a flight cage located in an observation room with a one-way mirror. The photoperiod was kept on a 12:12 L:D (light:dark) schedule until 1 Dec. 1992, when it was increased gradually to 16:8 L:D by 2 Jan. (maintained until 24 March when the hybrid began molting) to stimulate singing behavior and breeding condition.

Between 7 Nov. 1991 and 19 Feb. 1992, we recorded vocalizations of the hybrid over 27 hours using a Nagra IV tape recorder (15 cm/sec speed). Duration (wide band; 600 Hz) and minimum and maximum frequency (narrow band; 117 Hz) of vocalizations were analyzed using a Kay Electrometrics DSP Sonagraph Model 5500. Vocalizations were recorded during undisturbed observation, elicited via playback experiments, or by introducing individuals of parent species captured using Potter traps on the zoo grounds. Birds placed in the hybrid's cage included three male White-throated Sparrows (one each day for a half hour on 7, 8, and 15 Nov. 1991) and a female White-throated Sparrow and Dark-eyed Junco concurrently for 15 min on 22 March 1992.

Playback experiment.—We wanted to test the hybrid's species recognition abilities and used a playback experiment to determine if the hybrid responded differently to its own song as compared to its parent species' songs and the song of a different species (Wood Thrush [*Hylocichla mustelina*]). We rotated the presentation of four songs in trials conducted for 17 days between 23 Jan. and 3 March 1992, with up to three playback experiments per day between 9:00–10:30, 13:30–14:30, and 16:30–17:30. The latter three species' songs, each representing one individual, were taken from Peterson (1983), with the sparrow and thrush recorded in New York and the junco in Maine. REJ recorded the hybrid's behavior for five min each before, during, and after the playback. Each playback lasted one min (the first minute of the "during" part of the trial), consisting of six songs separated by eight seconds. Nine playback trials per song type were conducted, with three trials in each of the time periods. Behaviors recorded were the number of flights, hops, tseet calls, bill wipes, preening and eating bouts, and time spent perched.

For each behavior, we first used an analysis of covariance (ANCOVA; Norusis 1988) to test for differences in behavioral response ("during") among the playback types, with time as a factor and the behavioral score "before" playback as a covariate (to take into account the hybrid's previous activity level). When we found that time was nonsignificant for all behaviors (except eating) and that the covariate "before" was significant for all (Fs > 5.97, df = 1,23, Ps < 0.02) but two behaviors (preening and bill wipes), we decided to use the difference in behavior ("during" minus "before" playback) in one-way ANOVAs employing the least significant difference (LSD) procedure for pairwise comparisons among playback types.

Interactions with parental species.—We tested whether the hybrid showed a difference in behavior toward male and female pairs of the two parent species. Between 15 March and 16 April, we conducted up to two fifteen minute trials per day (between 09:00–11:00 and 15:00–17:00 EST) in which one male junco and one male sparrow, or one female junco and one female sparrow, were placed in small cages adjacent to and on either side of the hybrid's cage. These birds were captured using mist nets or Potter traps in Potomac, Maryland, and Washington, D.C., and were released after trials. We alternated the presentation of males and females as well as the species' position on either side of the hybrid's cage. To avoid bias in the hybrids' movements, its cage was arranged symmetrically with food dishes placed on the floor in the center of the cage.

Trials were videotaped, and data were collected from the recordings. REJ recorded the same behaviors listed above occurring on the right and left sides of the cage. Total time

spent on the right and left sides of the cage was also recorded (excluding time spent eating). To determine if the hybrid's response was consistent, we first used the same male and female pair for six trials each. For the remaining trials, we tested individual pairs only once, each pair consisting of new individuals, for a total of seven male and six female pairwise tests (including the first trials of the male and female pairs used in the consistency test). For each sex, we tested whether the hybrid responded differently to the two species using a sign test (Norusis 1988).

Reproductive condition and mitochondrial DNA analyses.—Haldane's (1922) rule states that in hybrids the heterogametic sex (in birds, females) will tend to be absent or infertile, whereas the homogametic sex (males) will be fertile. On 31 Jan. and 27 March, ESM conducted cloacal lavages (see Quay 1984) to ascertain whether the hybrid was fertile. All slides were sent to W. B. Quay to determine presence of sperm.

Mitochondrial DNA was sequenced from the hybrid, two Dark-eyed Juncos, and two White-throated Sparrows. MtDNA exhibits maternal inheritance in birds; thus, the mtDNA haplotype of the hybrid indicates which of the two putative parental species was its mother. Genomic DNA was isolated from whole blood using a standard protocol of cell lysis, proteinase K digestion, followed by phenol-chloroform extraction and ethanol precipitation. The DNA was hooked from solution and dialysed centrifugally. A small amount of the purified DNA (<100 ng) was used as a template for amplifications via the polymerase chain reaction (PCR). Two primers flanking part of the cytochrome *b* gene (Kessing et al. 1989) were chosen: cytochrome *b*1 (5′-AACATCTCAGCATGATGAAA-3′) and cytochrome *b*2 (5′-CAGAATGATATTTGTCCTCA-3′). We had found that these amplify the appropriate region from the mtDNA of passerine birds. PCR was carried out in 50 μl volumes containing template DNA, *Taq* polymerase buffer, deoxynucleotide triphosphates, primer, and *Taq* polymerase following the protocol of Palumbi et al. (1991). The PCR was run for 35 cycles with the following standard conditions: 92°C denaturation for 1 min, 50°C primer annealing for 1 min, and 72°C extension for 3 min. Products were electrophoresed in a 2% low-melting point agarose minigel in 1× TBE and visualized by staining with ethidium bromide. Appropriate bands were cut from the gel with a scalpel and the product was purified from the gel slice using a NaI/glassmilk kit (Geneclean, Bio101). We sequenced the double-stranded product by the protocol of Palumbi et al. (1991) using the USB Sequence 2.0 kit. Sequencing reactions were denatured for about 5 min at 95°C and loaded onto an 8% polyacrylamide-TBE-urea denaturing gel. The gel was run for 2.5 to 6 hours at about 1500 V, depending on how far from the primer we wanted to obtain sequence. The gel was soaked in a methanol-acetic acid bath for 30 minutes and dried at 80°C on a gel drier under vacuum. The dried gel was exposed to Xomat-RP film for 1–4 days to obtain the sequence. Sequences were read and aligned with MacVector 3.5 (IBI 1991).

RESULTS

Vocalizations.—The hybrid's notes 1 (tseet) and 29 (chip, Stefanski and Falls 1972) resembled White-throated Sparrow call notes (Fig. 1). Tseet (note 1; Fig. 1) was the hybrid's most common vocalization.

The hybrid also used several junco call notes. The hybrid's note 2 (Fig. 1) was very similar to the Dark-eyed Junco tsip and trill (the hybrid uttered one trill of thirteen 2 notes) recorded by Balph (1977). Other hybrid notes (4, 6, 25, 30; Fig. 1) resembled junco notes (respectively, zeet, kew, chit, and warble in Balph 1977).

We first recorded the hybrid singing both a mixed song of junco and

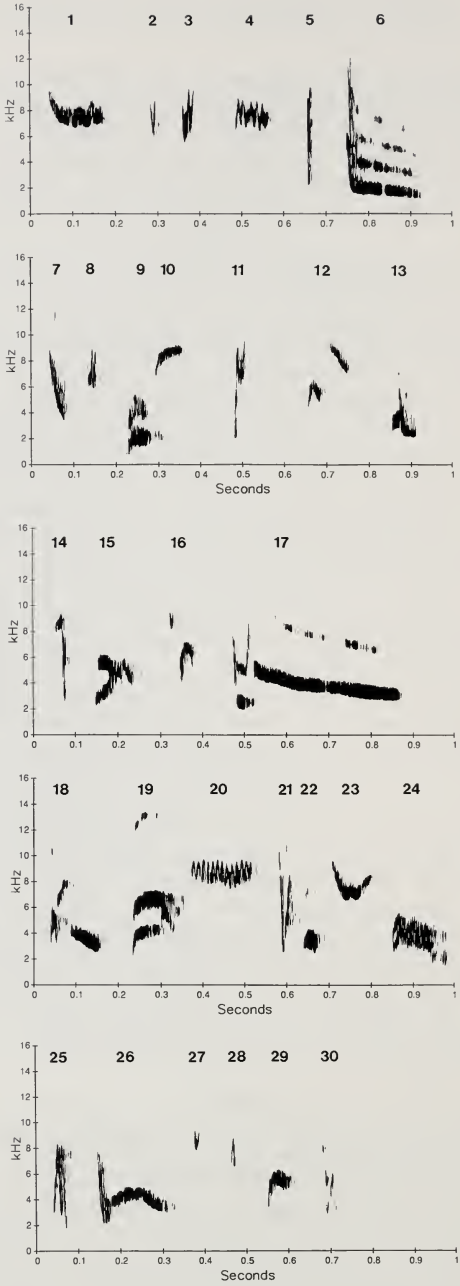

FIG. 1. Long song notes of the *Zonotrichia albicollis* × *Junco hyemalis* hybrid. Notes 1 (tseet) and 29 (chip) resemble White-throated Sparrow notes. Notes 2 (tsip, or trill when sung in sequence), 4 (zeet), 6 (kew), 25 (chit), and 30 (warble) resemble Dark-eyed Junco notes.

sparrow notes and a "long song" on 8 Jan. 1992. The long song (Fig. 1; duration and frequency values in Table 1) could not be considered a subsong, defined by Marler et al. (1962:20) as a "long, rambling, and variable series of sounds," because it consisted of 30 repeated and relatively non-variable notes. The long song notes were often sung in the sequence shown in Fig. 1 (with notes 1, 2, 3, 4, 6, 7, 8, 14, 16, and 18 repeated two times or more, and notes 19 and above sung infrequently). However, variation in the sequence and in the number of note repetitions was apparent.

The hybrid's song was a junco-like trill (3 notes per syllable, Konishi 1964) followed by zero (N = 6), two (N = 6), three (N = 12), or four (N = 1) sets of White-throated Sparrow-like "peabody" notes (Fig. 2). A total of 25 songs was recorded. The hybrid's "peabody" notes were not as distinctly separated as those of White-throated Sparrows (Fig. 2; see Borror and Gunn 1965); most (33/52; 63%) sounded like unbroken whistles. We did not attempt to compare statistically the hybrid's song with parent species' song. Geographic variation in the parent species' songs and the unknown origin of the hybrid make it difficult to obtain appropriate parental songs for comparison with the hybrid's song. Qualitatively, the two parts of the hybrid's song sounded like the two parent species' songs, which are quite distinct from each other (trill versus whistled notes). In the literature, some frequency and duration measurements of junco (Konishi 1964) and sparrow (Waas 1988) song seem indistinguishable from those of the hybrid.

Playback experiment.—One-way ANOVAs of difference scores ("during"—"before" playback) showed that the hybrid responded significantly differently to the four playbacks in number of tseets ($F = 5.10$, df = 3,32, $P = 0.005$) and eating bouts ($F = 4.73$, df = 3,32, $P = 0.008$), and possibly time spent perched ($F = 2.83$, df = 3,32, $P = 0.054$). One-way ANOVA LSD comparisons significant at $P < 0.05$ showed that the hybrid flew more in response to the hybrid playback than to the thrush, tseeted more in response to the hybrid than the junco and thrush, ate more in response to the junco than to the hybrid, sparrow, and thrush, perched more in response to the sparrow than the hybrid, and preened more in response to the thrush than the sparrow (Table 2). The hybrid responded most actively to its own song in number of flights and tseets, and least actively to the thrush song. As shown at the bottom of Table 2, the hybrid in general showed decreasing activity in response to playbacks in the order hybrid > junco = sparrow > thrush.

Interactions with parental species.—The hybrid was subordinate to the first two and dominant over the third male White-throated Sparrow introduced into its cage. During these encounters, the hybrid exhibited four

Table 1

Descriptive Statistics for the White-throated Sparrow × Dark-eyed Junco Hybrid's Vocalizations

Note	Duration ($\bar{x}$ ± SD)	Max. frequency ($\bar{x}$ ± SD)	Min. frequency ($\bar{x}$ ± SD)	N
1	0.16 ± 0.026	10,117 ± 628.2	6734 ± 350.9	23
2[b]	0.02 ± 0.002	8952 ± 571.4	6120 ± 178.8	20
3	0.03 ± 0.003	9177 ± 340.3	6309 ± 155.9	19
4[c]	0.09 ± 0.008	9032 ± 213.4	6805 ± 228.2	15
5	0.15 ± 0.002	8977 ± 686.5	2943 ± 614.4	21
6[d]	0.09 ± 0.006	5860 ± 188.2	1338 ± 48.1	27
7	0.03 ± 0.003	9371 ± 306.7	4133 ± 262.8	18
8	0.02 ± 0.002	9275 ± 212.0	6059 ± 183.8	15
9	0.05 ± 0.005	2800 ± 140.1	1575 ± 130.5	16
10	0.08 ± 0.004	9035 ± 194.1	7040 ± 285.3	15
11	0.03 ± 0.002	9473 ± 210.8	4587 ± 1094.5	6
12	0.10 ± 0.005	9473 ± 279.4	4791 ± 215.2	18
13	0.06 ± 0.005	5419 ± 366.6	2379 ± 89.3	16
14	0.03 ± 0.002	9033 ± 162.0	2856 ± 264.9	17
15	0.06 ± 0.005	5419 ± 366.6	2379 ± 89.3	16
16	0.06 ± 0.003	9548 ± 178.4	4711 ± 290.4	13
17	0.40 ± 0.025	5381 ± 116.0	2464 ± 96.6	15
18	0.12 ± 0.006	7940 ± 84.4	2927 ± 96.2	12
19	0.10 ± 0.010	6777 ± 116.1	2637 ± 384.1	14
20	0.14 ± 0.014	9416 ± 202.4	7672 ± 188.4	10
21	0.03 ± 0.003	8594 ± 819.7	2694 ± 307.7	14
22	0.04 ± 0.003	4044 ± 171.1	2000 ± 446.5	11
23	0.10 ± 0.007	10,061 ± 488.5	6715 ± 140.6	17
24	0.11 ± 0.011	5381 ± 206.9	1854 ± 176.6	17
25[e]	0.03 ± 0.007	8093 ± 23.1	2480 ± 692.8	3
26	0.18 ± 0.008	8160 ± 226.3	2340 ± 198.0	2
27	0.01 ± 0.001	9747 ± 334.7	8556 ± 383.9	9
28	0.02 ± 0.006	8140 ± 480.8	6280 ± 735.4	2
29	0.05 ± 0.005	6028 ± 200.6	3852 ± 491.1	8
30[f]	0.04	8280	3080	1

[a] Footnotes [b–f] show duration and frequency values for comparable Dark-eyed Junco vocalizations (Balph 1977; N = 10).
[b] tsip: duration = 0.02 ± 0.001 sec, maximum frequency = 10,550 ± 526 Hz, minimum frequency = 6580 ± 391 Hz.
[c] zeet: 0.09 ± 0.015, 9340 ± 123, 7380 ± 247.
[d] kew: 0.06 ± 0.010, 7560 ± 439, 1550 ± 71.
[e] chit: 0.02 ± 0.003, 7540 ± 321, 2920 ± 278.
[f] warble: 0.07 ± 0.030, 7400 ± 841, 3340 ± 1492.

→

Fig. 2. Songs of (A) Dark-eyed Junco, (B) White-throated Sparrow × Dark-eyed Junco hybrid, and (C) White-throated Sparrow. The sparrow and junco songs are taken from Peterson (1983).

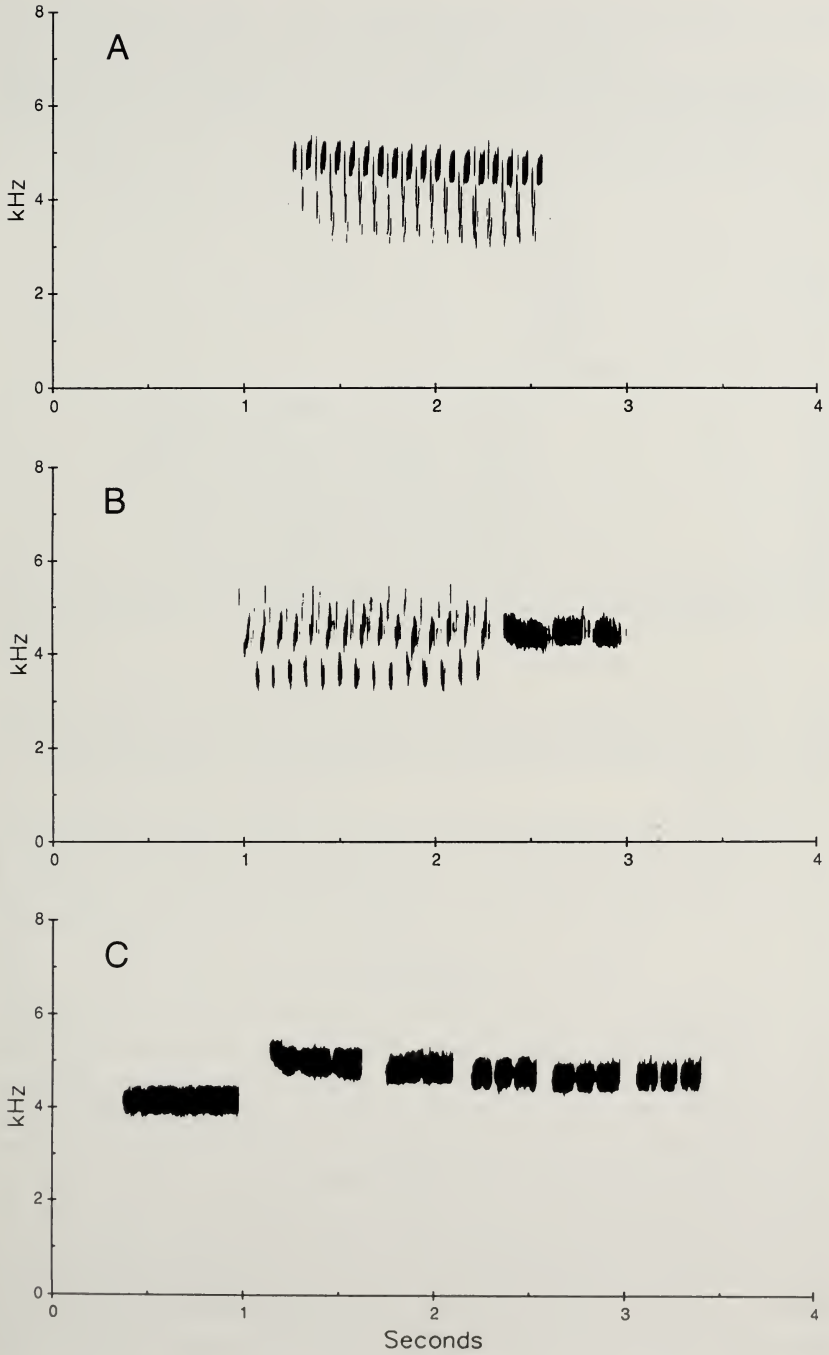
A
B
C
kHz
0
2
4
6
8
0
1
2
3
4
Seconds

TABLE 2

SIGNIFICANT ($P < 0.05$) ONE-WAY ANOVA LSD PAIRWISE COMPARISONS IN PLAYBACK EXPERIMENTS COMPARING THE WHITE-THROATED SPARROW × DARK-EYED JUNCO HYBRID'S RESPONSE TO ITS OWN SONG, ITS PARENT SPECIES' SONGS, AND A WOOD THRUSH SONG[a]

	Hybrid	Junco	Sparrow
Junco	Tseet + Eat −		
Sparrow	Perch −	Eat +	
Thrush	Fly + Tseet +	Eat +	Preen −

Group means in descending order:

Fly	Hybrid* > Junco > Sparrow > Thrush*
Tseet	Hybrid* > Sparrow > Junco* > Thrush*
Eat	Junco* > Hybrid* > Sparrow* > Thrush*
Hop	Hybrid > Junco > Sparrow > Thrush
Perch	Sparrow* > Thrush > Junco > Hybrid*
Preen	Thrush* > Hybrid > Junco > Sparrow*
Bill Wipe	Hybrid > Junco > Thrush > Sparrow

[a] + or − signifies greater or lesser behavioral activity in response to the playback song listed across the top.
* Indicates significant difference.

junco visual communication behaviors as described by Balph (1977): flight pursuits with tail-flashing, escape behavior, fluffed posture, and pecking attack.

The hybrid responded consistently over six trials to the same-individual male or female parental species pairs, showing no difference in response to the male sparrow versus junco, but spending more time (in all six trials, sign test, $P = 0.031$; $\bar{x} = 85\%$ more) and tseeting more ($P = 0.031$; $\bar{x} = 86\%$ more) on the side with the sparrow female as compared to the side with the junco female. Comparing all independent pairwise tests (males, N = 7; females, N = 6), the hybrid again showed no significant differences in behavior toward the male sparrows as compared to the male juncos. However, in all six trials (sign test, $P = 0.031$) the hybrid spent more time ($\bar{x} = 83\%$ more) and flew (83% more), tseeted (91% more), and preened (92% more) more frequently on the side with the sparrow females than on the side with the junco females.

When trials with the first two females used in the consistency test were finished, we placed these females into the hybrid's cage simultaneously for 15 min. The hybrid was not successful in mounting either female despite 58 flights toward or displacements of the sparrow and 24 of the junco ($\chi^2 = 14.1$, df = 1, $P < 0.001$). While interacting with the female

junco, the hybrid three times used a junco courtship display ("head dance," Sabine 1952) consisting of vertical head thrusts.

Reproductive condition and mitochondrial DNA analyses.—W. B. Quay found no sperm in the lavage slides. Testes size of the hybrid was 2 × 1.5 mm (Phil Angle, National Museum of Natural History, pers. comm.). The bird was in nonbreeding condition following post-breeding molt when the testes were measured.

A total of 231 bp of sequence was generated for the hybrid sparrow (Fig. 3). Of these, 9 bp were classified as ambiguous because two lanes (generally C and T or A and G) had bands rather than the expected single lane. We do not know the reason for these ambiguities; they could result from heteroplasmy, a nuclear homologue, contamination, or sequencing artifacts. The ambiguous bases did not result from a combination of each parental haplotype in the hybrid (Fig. 3). The hybrid's sequence was aligned to the sequences of the White-throated Sparrow and the Dark-eyed Junco. We found six substitutions between the sparrow and junco sequences representing a proportional sequence difference of 2.6%. This value is only about half the divergence that Zink et al. (1991) found using restriction fragment length polymorphism analysis of the entire mtDNA molecule.

Five of these six differences were also found between the hybrid and the junco sequence; the sixth was an ambiguous base in the hybrid (Fig. 3). On the other hand, the hybrid sequence was identical to that of the sparrow, indicating that the mtDNA of the hybrid was derived maternally from a White-throated Sparrow.

The hybrid died in captivity on 9 July 1992, and the skin is housed at the National Museum of Natural History (USNM 608306). Slides of the hybrid are accessioned at Visual Resources for Ornithology (VIREO VO6/13/001-005).

DISCUSSION

As far as we know, this is the first time that any hybrid songbird has been shown to use a mixed song, incorporating both parent species' songs into its own. Mixed songs have previously been reported only in pure species, involving closely related species (see Lemaire 1977:228 and refs. therein), presumably due to imprinting during a sensitive period. In several of these cases, species with mixed song were located in areas where hybridization occurred. That pure species can incorporate heterospecific song into their own songs indicates the importance of individual experience and learning. The mixed song of the hybrid, therefore, need not have been entirely genetically-based.

The hybrid's song and several call notes (two calls stemming from

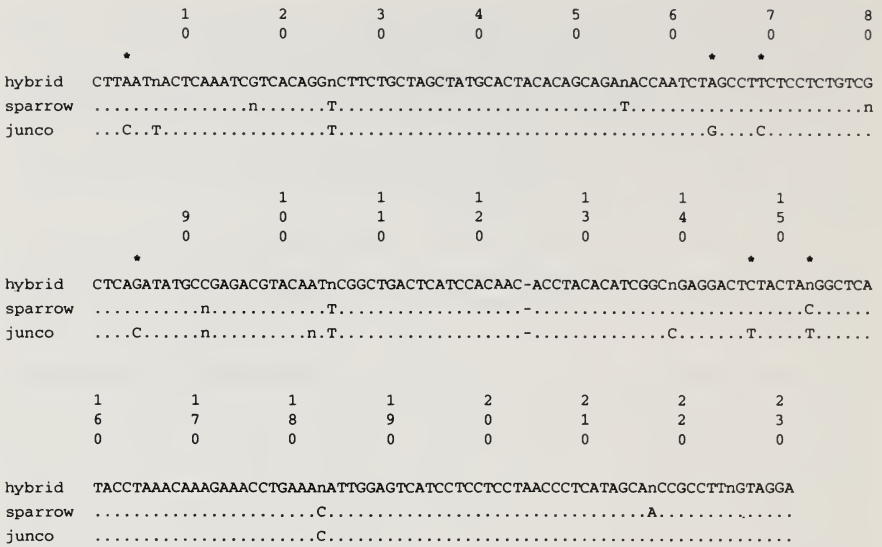

FIG. 3. Sequences of the two putative parental species and the hybrid individual for 231 bases of the cytochrome *b* gene of mtDNA. The sequences represent 124 bp corresponding to bases 15,012 to 15,136 of the chicken mtDNA (Desjardins and Réjean 1990) and 107 bp corresponding to bases 15,179 to 15,286. The "-" between bases 124 and 125 indicates the break between the two regions. A period (.) indicates that the base is identical to the hybrid's sequence; "n" indicates an ambiguous or unreadable base. The asterisks indicate bases that differ between the Dark-eyed Junco and the White-throated Sparrow.

sparrows and six from juncos) were similar in sonographic shape to parent species' vocalizations. The hybrid used parent species' vocalizations that are important in various behavioral contexts (e.g., song, tseet as a contact call, and kew and zeet used in agonistic encounters, Balph 1977). The hybrid's trill and warble notes, heard only once, are vocalizations which juncos use in complex bill-up or head dances (Balph 1977). Vocalizations are described for one other White-throated Sparrow × Dark-eyed Junco hybrid (Peacock 1956), which used sparrow "tseet" and distress calls.

We are unable to state whether we recorded the hybrid's entire repertoire. We did not observe the hybrid to use certain parent species' vocalizations (e.g., chack of junco, Balph 1977, or distress call of sparrow, Stefanski and Falls 1972). This may indicate (1) lack of behavioral context in the laboratory, (2) that some calls are infrequently used and hence not learned or used much by hybrids, or (3) that behaviorally important calls tend to be components of an "inherited pattern of motor output . . . (or) an inherited auditory 'template'" (Marler 1963:233). However, unlike the song, the hybrid's call notes did not appear to be mixtures of the

parental species' call notes. Some of the call notes were produced in the correct contexts for their use or were incorporated into the long song. Overall, it appeared that the hybrid had more note types than either parental species.

The hybrid responded most to its own song, least to the thrush song, and showed no clear difference in response to the sparrow vs junco songs. Indigo Bunting (*Passerina cyanea*) × Lazuli Bunting (*P. amoena*) hybrids responded similarly to song playbacks of the two parent species (Baker 1991), and Emlen et al. (1975) found that Indigo and Lazuli buntings with mixed songs responded to songs of both species. In another case, a Blue-winged (*Vermivora pinus*) × Golden-winged (*V. chrysoptera*) warbler hybrid did not respond to playbacks of one of its parent-type songs (Murray and Gill 1976). Learning environment probably plays a role in the development of a hybrid's response to its parent species. Because our experiment tested only one individual's song for each species (and only one hybrid), our results represent only one condition (Kroodsma 1989). As well, we may have used song types of the sparrow or junco which were unfamiliar to the hybrid, thereby affecting its response. In any case, the hybrid should have responded strongly to any song type of the parental species whose song had greater salience (cf Morton 1986). The fact that it responded most actively to its own song suggests that both parent species' songs were salient.

Based on mtDNA, the hybrid's mother was a White-throated Sparrow. This finding suggests several things. First, maternal imprinting by the hybrid upon its sparrow mother may explain the hybrid's preference for female sparrows over juncos. Second, because the hybrid's song is more junco-like (especially when sung without "peabody" notes), the template may have been inherited paternally from its junco father. Alternatively, the hybrid may have originated in an area where juncos are more common than sparrows; Gelter (1987) found that hybrid Pied (*Ficedula hypoleuca*) × Collared (*F. albicollis*) flycatcher songs more closely resembled songs of the species with the higher population density in the area. Whether the White-throated Sparrow × Dark-eyed Junco hybrid resulted from an extra-pair copulation or a pair bond is unknown.

The hybrid was captured in a net adjacent to one with a White-throated Sparrow (Donnald and Maane 1992). Other hybrids were noted to have been foraging with White-throated Sparrows (Peacock 1956, Hamilton and Hamilton 1957, Eastman and Eastman 1966, Snyder 1967). That these hybrids may preferentially associate with sparrows over juncos is strengthened by our observations that the hybrid used the sparrow "tseet" vocalization most frequently and preferred female sparrows over female juncos.

Sparrow × junco hybrids are relatively rare, and it is unknown whether these hybrids arise from a regular zone of hybridization (such as where one or both of these species is rare, e.g., southern Ontario, Peck and James 1987) or whether they originate from anywhere within the large overlapping breeding range area for these two species. The hybrid began singing on a 16:8 L:D photoperiod (on the summer solstice, 16 h of light occurs at 48° north latitude, George H. Kaplan, U.S. Naval Observatory, pers. comm.), which coincides with southern Canada. One immature hybrid was found in St. Thomas, Ontario, and most of the other hybrids were found in eastern U.S. coastal states.

According to Haldane's (1922) rule, avian hybrid males should be fertile (Gelter et al. 1992; but see Read and Nee 1991). We were unable to ascertain conclusively whether our male hybrid was fertile, but negative results from two cloacal lavages suggest infertility. The size of the hybrid's testes post-mortem were typical of sparrows and juncos during the nonbreeding season. However, two other adult male sparrow × junco hybrids were noted as having small (≤ 1 mm) or missing testes (Hamilton and Hamilton 1957, Short and Simon 1965) outside the breeding season.

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This paper is dedicated to the beautiful hybrid whose song and spirit live on. We especially thank M. T. Donnald for catching the hybrid and bringing it to us for study, and M. V. Deal, J. C. Harris, F. B. Kohn, and C. E. Mathias for taking care of it. R. M. Zink kindly sent us mtDNA information. We are grateful to M. T. Donnald and S. B. Strange, for helping catch birds for trials, and to W. B. Quay for examining lavage samples. REJ was supported by the Friends of the National Zoo and the Dept. of Zoological Research during the study. Thanks to T. Garland, Jr. for discussions of experimental design, to J. C. Pinheiro for statistical help, and to T. Garland, Jr., K. C. Derrickson, and reviewers for improving the manuscript.

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COLOR PLATE

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HABITAT CHARACTERIZATION OF SECONDARY CAVITY-NESTING BIRDS IN OKLAHOMA

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Abstract.—We analyzed vegetation structure at potential and actual nest sites of secondary cavity-nesting birds in south-central Oklahoma. Habitats consisted of old fields with remnants of tallgrass prairie and patches of post oak-blackjack oak (*Quercus stellata, Q. marilandica*) woodland. During the 1989 and 1990 breeding seasons, 194 sites with nest boxes were analyzed, including those occupied by Bewick's Wrens (*Thryomanes bewickii*), Carolina Chickadees (*Parus carolinensis*), Tufted Titmice (*P. bicolor*), Eastern Bluebirds (*Sialia sialis*), House Sparrows (*Passer domesticus*), and some not used by birds. Principal-components analysis was employed to describe general vegetational gradients and stepwise discriminant analysis to delineate differences in nest-site habitats among species. Through use of appropriate indices and Monte Carlo simulations, niche breadth and overlap were assessed relative to a habitat gradient (principal component I) extending from open areas to woodlands. Chance expectations were established assuming that the nest boxes represented a limited resource, albeit one that was not fully utilized during the course of the study. Eastern Bluebirds and House Sparrows chose nest boxes in open areas with few trees, Bewick's Wrens selected boxes in wooded areas with junipers and few deciduous trees other than oaks, Carolina Chickadees most often were found in areas with junipers and oaks, and nest boxes used by Tufted Titmice were broadly distributed, not showing association with any particular habitat type. Niche overlap for Eastern Bluebirds and House Sparrows was more pronounced than expected by chance. These two species showed less overlap with Bewick's Wrens, Carolina Chickadees, and Tufted Titmice than expected given simulation results. For the House Sparrow and Eastern Bluebird, which were restricted to open habitats, niche breadth was significantly less than expected by chance. Likewise, niche breadth for the Bewick's Wren, with the majority of its nests being in semiopen areas, was less than predicted. For Carolina Chickadees and Tufted Titmice, nest-box use relative to the habitat gradient represented by principal component I was not different from random expectations. Our findings indicate that the introduced House Sparrow potentially can negatively influence nesting success of Eastern Bluebirds given that preferences for nest sites of the two species correspond so closely. Direct observations of House Sparrow and Eastern Bluebird interactions indicate that in some cases bluebirds are detrimentally affected. *Received 11 Feb. 1993, accepted 15 Oct. 1993.*

Habitat can be defined in a narrow sense as a spatially contiguous vegetation type that appears more or less homogeneous throughout and is physiognomically distinctive from other such types (Hutto 1985). Avian habitats include foraging, singing and nesting sites that can be defined by their associated structural and floristic properties. James (1971) assessed habitats of breeding birds on the basis of several structural attributes of the vegetation, which taken together describe the "niche-gestalt" for a species. A number of studies have shown strong associations between

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bird-species occurrence and structural aspects of the vegetation (e.g., MacArthur and MacArthur 1961, James 1971, Rotenberry 1981, James and Wamer 1982). Habitat selection in birds has been thought to be a result of a species' response to the configuration of the vegetational components of the environment (e.g., Hilden 1965, Ficken and Ficken 1966, Klopfer 1969, Wiens 1969, Cody 1985).

Early quantitative studies of avian habitats described vegetation characteristics of plots centered on perches of singing territorial males (e.g., James 1971, Whitmore 1975, Smith 1977). In addition, some investigators have evaluated foraging and nesting sites within the breeding territory (e.g., Morrison and Meslow 1983, Willner et al. 1983, Holway 1991, Sakai and Noon 1991). Although the breeding habitats characterized by data from song-perch sites may provide a useful perspective, habitat evaluation of other bird activity sites is of interest to compare and contrast aspects of habitat use. Collins (1981) found that areas at song-perch sites and those at nest sites differed significantly for several warbler species. His and subsequent studies have shown that characteristics of nesting sites of avian species, in addition to those for other activity sites, can provide a more complete picture of avian breeding habitats.

Cavity-nesting birds provide an ideal group for evaluating nesting habitats. For example, Conner and Adkisson (1976, 1977) quantitatively assessed habitat use by woodpecker species, delineating important macrohabitat properties and those of microhabitats in the vicinity of nest cavities. Many secondary cavity-nesting birds (i.e., those that do not excavate their own cavities) readily use nest boxes. One can appraise nesting-habitat preferences of these species by describing immediate nest-box surroundings. Here we evaluate the habitat use of five secondary cavity-nesting bird species in south-central Oklahoma: Bewick's Wren (*Thryomanes bewickii*); Carolina Chickadee (*Parus carolinensis*); Tufted Titmouse (*P. bicolor*); Eastern Bluebird (*Sialia sialis*); and House Sparrow (*Passer domesticus*). Our purpose is to use interspecific comparisons to provide a more complete understanding of the important factors influencing habitat use by cavity-nesting species. The study design also allows us to assess indirectly possible influences of an introduced species, the House Sparrow, on nesting of native birds.

METHODS

Study sites.—Five sites (254 ha total) in two areas were studied during the 1989 and 1990 breeding seasons. One area, containing a single study site (64 ha), was on the grounds of the University of Oklahoma Biological Station (UOBS) in Marshall County. The second area included four study sites (190 ha total) and was located 11.3 km northeast of Ada, Pontotoc County, Oklahoma, approximately 118 km north of the first area. The four sites near Ada varied in size from 16 to 120 ha. All sites were characterized as old fields con-

taining remnants of tallgrass prairie, woody plants (including eastern red cedars, *Juniperus virginianus,* and winged elms, *Ulmus alata*), and patches of post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*) woodland. Based on a preliminary quantitative assessment of vegetation data, as well as our familiarity with the two study areas, it was clear that they were very similar in vegetation characteristics; thus, data were combined for analyses. These sites were selected because they were representative of typical habitats of the region.

Nest boxes were classified as having been used by a bird species if nest building was completed and egg laying begun. The remaining boxes were categorized as unoccupied. For the UOBS site, which was evaluated only in 1989, 12 nest boxes were used: Bewick's Wren, 2 boxes; Carolina Chickadee, 1; Tufted Titmouse, 2; Eastern Bluebird, 5; and House Sparrow, 2. For the Ada sites, 182 potential nest sites were evaluated for habitat characteristics (see below) in the 1989 and 1990 breeding seasons, including nest boxes used by Bewick's Wrens (16), Carolina Chickadees (14), Tufted Titmice (17), Eastern Bluebirds (45), and House Sparrows (7), as well as 83 unoccupied boxes in 1990. Thirty-two nest boxes were used by more than one species during the breeding season and, thus, were entered into the analysis twice. Given that we have been conservative in our interpretation of statistical tests, this procedure is not likely to have significantly altered our conclusions.

Sampling techniques.—Nesting habitats were assessed by evaluating vegetation characteristics of 0.04-ha (0.1-acre) circular plots centered on 162 nest boxes placed in predetermined locations along the forest edge in south-central Oklahoma. The nest boxes (Oklahoma Dept. of Wildlife Conservation Nongame Program, 1986 pamphlet) had internal dimensions of 10.2 × 10.2 × 25.4 cm, with an entrance hole 3.8 cm in diameter. Nest boxes were placed on metal *T*-posts 1.2 to 1.5 m above the ground with the entrance hole oriented in a random direction. The circular-plot method developed by James and Shugart (1970) was used to quantify vegetation structure of the area surrounding the nest boxes. Each 0.04-ha circular plot was centered on a nest box. We also monitored the boxes weekly and recorded the number of eggs laid and hatched, as well as the number of young fledged.

Within each plot, we recorded (1) number of trees with diameters at breast height (dbh) greater than or equal to 7.6 cm; (2) number of shrub stems (<7.6 cm dbh) intercepted by a 1.52-m rod passed horizontally through vegetation at a height of 1 m along two orthogonal transects; and (3) ground-cover types at 20 points spaced 2 m apart along two orthogonal axes. The orientation of orthogonal axes for each plot was chosen randomly (using a random-number table). We calculated relative densities, basal areas and relative dominances (see Table 1) for several categories of trees including oaks, other deciduous tree species, and junipers. We also calculated shrub stem counts per unit area and percent ground cover.

To obtain vertical profiles of the vegetation, we passed a 7.5-m telescoping pole vertically through the vegetation at 20 points spaced 2 m apart along two orthogonal axes. We recorded the number of decimeter intervals with tree hits for 11 height-class intervals. At each of the 20 points, we also recorded the maximum height of the canopy. The vegetational inventories were completed at nest boxes during a six-week period from 21 May to 7 July in 1989 and 1990. The 40 vegetation variables evaluated and their abbreviations are listed in Table 1.

Principal-components analysis.—We employed principal-components analysis to characterize general trends along orthogonal vegetational gradients. Calculations were carried out using the computer package NT-SYS (Rohlf et al. 1982). From a matrix of correlations among 40 vegetation variables, major trends were represented on composite principal-component axes (Sneath and Sokal 1973). The first three components are orthogonal composite axes that explain progressively the maximum possible portion of the remaining character variance. None of the remaining principal components had eigenvalues greater than 3.00. Correlations (i.e., loadings) of original variables with principal components were generated, and component scores of each sample plot were projected onto the components. Before

Table 1

Vegetation Variables Computed for Nesting-habitat Plots. Variable Number, Code, Description, and Units of Measure Given[a]

No.	Code	Vegetation variable
1–3	OAKA-OAKC	Number of oaks with dbh >7.5–22.5 cm, >22.5–52.5 cm, and >52.5 cm, respectively (/ha)
4–6	NONA-NONC	Number of nonoaks with dbh >7.5–22.5 cm, >22.5–52.5 cm, and >52.5 cm, respectively (/ha)
7	JUNA	Number of junipers with dbh >7.5 cm (/ha)
8–10	DENSO, DENSN, DENSJ	Relative density of oaks, nonoaks, and junipers (percent = 100[no. oaks/total no. trees])
11–13	BAOAK, BANON, BAJUN	Basal area of oaks, nonoaks, junipers (cm^2/ha)
14–16	RDOAK, RDNON, RDJUN	Relative dominance of oaks, nonoaks, junipers (percent = 100[basal area oaks/total basal area])
17	VARQUAD	Variation (SD) in trees per quadrant (cm^2/ha)
18–22	STEMO, STEMN, STEMJ, STEMV	Number of oak, nonoak, juniper and vine stems at 1.5-m height (/ha)
22–27	WOODYCOV, FORBCOV, GRASSCOV, LEAFCOV, ROCKCOV, BARECOV	Ground cover of woody plants, forbs, grasses, leaf litter, rocks, or bare (percent)
28–38	HITSA-HITSK	Number of decimeters with tree hits, respectively, in the following height interval: 0.0–0.5 m; >0.5–1.0 m; >1.0–1.5 m; >1.5–2.0 m; >2.0–2.5 m; >2.5–3.0 m; >3.0–3.5 m; >3.5–4.5 m; >4.5–5.5 m; >5.5–6.5 m; >6.5–7.5 m (circle)
39	CANHT	Mean maximum height of canopy (m)
40	VARCAN	Variation (SD) of maximum height of canopy (cm^2/ha)

[a] Arcsine transformation (Sokal and Rohlf 1981) used for variables 8–10, 14–16, 22–27; square root of basal area used on variables 11–13. Values for variables 22–38 based on 20 points placed 2 m apart along two 20-m orthogonal axes.

projection, the vegetation variables were standardized to a mean of 0 and standard deviation of 1 (Sneath and Sokal 1973).

Niche overlap and breadth.—We evaluated niche overlap and niche breadth relative to a habitat gradient extending from open areas to woodlands, which is represented (as detailed in the Results section) by principal component I. The habitat gradient represented by projections of the 194 nest boxes onto this component was subdivided into nine intervals, and we determined the number of nest boxes with projections from: (1) −0.74 to −0.5; (2) >−0.5 to −0.3; (3) >−0.3 to −0.1; (4) >−0.1 to 0.1; (5) >0.1 to 0.3; (6) >0.3 to 0.5; (7) >0.5 to 0.7; (8) >0.7 to 0.9; (9) >0.9 to 1.2. The numbers of nests for each species in each interval were tabulated.

Niche overlap was evaluated using the simplified Morisita index (M; Krebs 1989) proposed by Horn (1966):

$$M = \left(2 \sum_{i=1}^{n} p_{ij} p_{ik}\right) \Big/ \left(\sum_{i=1}^{n} p_{ij}^2 + \sum_{i=1}^{n} p_{ik}^2\right),$$

where p_{ij} is the proportion that resource i is of the total resources used by species j, p_{ik} is the proportion that resource i is of the total resources used by species k, and n is the total number of resource states. This index ranges from 0 when there is no overlap in resource use to 1 when there is complete overlap (when the two species use resources in equal proportions).

Niche breadth was assessed using Smith's index (B; Krebs 1989):

$$B = \sum_{i=1}^{n} (p_i a_i)^{0.5},$$

where p_i is the proportion that resource i is of the total resources used by the species and a_i is the proportion that resource i is of the total resources available, and n is the total number of resource states. This index ranges from near 0 when only a single resource state is used (i.e., minimum breadth) to 1 when all resources are used in proportion to their availability (maximum breadth).

A Monte Carlo simulation was employed to evaluate the degree to which the resulting coefficients differed in a significant way statistically from what one would expect by chance alone. We started with the 194 nest boxes distributed among the nine resource states and randomly drew the number of nests for species j and then the number of nests for species k; all were drawn without replacement. For the two groups of randomly drawn nests we then calculated the simplified Morisita index for niche overlap. This was compared with the value of the index for the two species as calculated from the actual samples of nests to determine whether the simulated value was less than the sample value, or greater than/equal to it. The simulation was repeated 1000 times and, based on the number of index values less than or greater than/equal to the sample value, we calculated the two-tailed probability that the sample value deviated from what would be expected by chance alone.

In a similar way we randomly drew from the 194 available nest boxes the number of nests for a given species without replacement and calculated the Smith index for niche breadth. As above, the simulation was repeated 1000 times, and we calculated the two-tailed probability that the sample value deviated from chance expectation.

Given that we are drawing without replacement the expected values for the simplified Morisita index and the Smith index increase as the numbers of nests in the samples increase. Thus, we are statistically evaluating whether a given value deviates significantly from the expected value for a given-sized sample.

Discriminant analysis.—Stepwise discriminant analysis (McLachlan 1992), also referred to by various authors as canonical-variates analysis, was used to determine the subset of the 40 vegetation variables that, in combination, maximally discriminated among sample plots for the different species, as well as for the unoccupied boxes. We used program 7M of the computer package BMDP (Dixon 1990) for calculations. As stated by Dixon (1990), the discriminant analysis in this program is one approach to one-way multivariate analysis of variance. Vegetation variables were selected that exhibited relatively high variation among species and low variation within species. Forward and backward stepping was used (i.e., variables were entered or removed from the classification function based on F-values). The F-to-enter a variable in the classification function was set at 4.0, while the F-to-remove was 3.996. Sample plots were projected onto the resulting canonical axes.

Classification functions were derived to assign plots to one of the groups, depending on

the relative probability of group membership. A given plot had an equal probability of being assigned to any one of the groups. Note this does not mean that an equal number of plots would be assigned to each group, but only that *a priori* we did not bias the possibility of a particular plot being categorized as representing one species or another. In fact, because sample sizes for species were unequal, more plots were assigned to some species than to others simply because plots had attributes that were characteristic of particular species. Measurement values for the plot were multiplied by coefficients of the classification function, and the resulting products added to the constants of these functions. The calculation was completed for all group members, and a plot assigned to the appropriate group, depending on which of the resulting classification values was the greatest (Schnell et al. 1986). We also used a true-jackknifed classification procedure, which effectively leaves out the individual plot being considered, recomputes coefficients of the functions, and then evaluates the plot. Typically, this procedure gives a better indication of the efficacy of functions to correctly allocate or identify new plots (i.e., those not used to compute the functions; Schnell et al. 1986).

As indicated by Morrison et al. (1992) and others, one must be judicious when interpreting discriminant analyses and other multivariate results where relatively small samples are involved for groups being evaluated. In our study the numbers of some species nesting in the area were relatively small. Thus, we have been cautious in our evaluation of discriminant analyses. Also, use of the jackknife procedure results in a conservative assessment of the degree of discrimination possible between species.

In order to assess the relationship, if any, between nest success and habitat measures, we plotted the percent fledged from eggs laid and percent fledged from eggs hatched against each of the three components. Least-squares regression analyses were used statistically to assess relationships.

RESULTS

Principal-components analysis.—The first 10 components had eigenvalues greater than one, while only the first four had eigenvalues greater than two. The first four principal components explained 56.2% of the total variance in vegetation variables, while the first three summarized 49.4%. Correlations of components with original variables and plot projections (Table 2, Figs. 1–3) indicate that component I (eigenvalue of 11.65; 29.1% of total variance) represents a gradient from open grassy areas (high negative loading for GRASSCOV) to oak forest areas (high positive loading for OAKB, BAOAK). In addition, the variables portraying vertical structure of the vegetation and percent ground cover of leaves (LEAFCOV, HITSE-HITSK, CANHT, VARCAN) exhibited high loadings on component I, reflecting the gradient from open to forested areas. Component II (eigenvalue of 4.29; 10.7% of total variance) represents a gradient of increasing numbers of deciduous species other than oaks (DENSN, BANON, RDNON; Fig. 1). No other vegetation variables exhibited high loadings (Table 2). The loadings and projections on component III (Table 2, Fig. 1), which explained 9.6% of the total variance (eigenvalue of 3.85), reflect a gradient from wooded areas with junipers and few oaks (JUNA, DENSJ, BAJUN, RDJUN, STEMJ) to areas having

oaks and few junipers (BAOAK, DENSO, RDOAK). Component IV (6.7% of total variance) is a gradient from wooded areas with deciduous trees other than oaks and with few junipers (STEMN, HITSA, HITSC) to wooded areas with junipers but with few deciduous trees other than oaks (DENSJ, RDJUN). The eigenvalue for component IV was 2.68, which indicates that less than the equivalent of three original variables is summarized. Thus, we have not included projections or detailed loadings for this component.

When considering species individually, the plots for the nest boxes occupied by Bewick's Wrens have a broad range on component I (Fig. 2A); however, most of them have relatively high values on component I, indicating an association of Bewick's Wrens with more wooded areas. On component II, two-thirds of the plots have negative projections, which indicates a degree of avoidance of areas with relatively large numbers of deciduous trees other than oaks. On component III, Bewick's Wren plots are dispersed along the axis; however, two-thirds of the plots have negative values, indicating some degree of affinity for areas with junipers (Fig. 2B). Thus, Bewick's Wren plots, typically, were located in forested areas with junipers and relatively few deciduous tree species other than oaks.

Carolina Chickadee nest boxes tended to be in more open areas containing relatively few trees, as indicated by projections on component I (Fig. 2C), although the affinity for open areas was not as pronounced as in the Eastern Bluebird (Fig. 3A) and House Sparrow (Fig. 3C). Chickadee plots are widely distributed on component II (Fig. 2D), suggesting that this species shows no preference with respect to deciduous species other than oaks. However, chickadee plots have intermediate values on component III, indicating a preference for areas with mixed junipers and oaks (Fig. 2D). In general, Carolina Chickadee plots were found in open areas interspersed with juniper and oak trees. The broad distribution of Tufted Titmouse plots on component I (Fig. 2E) indicates no preference for open or forest habitats. However, 72% of the nest boxes used by Tufted Titmice have positive values on component III (Fig. 2F), indicating they were found in areas with oaks and relatively few junipers.

Plots occupied by Eastern Bluebirds are concentrated in grassy areas with few trees, as indicated by projections on component I (Fig. 3A). Not unexpectedly, given their known preference for open areas, no strong associations with deciduous trees or junipers are demonstrated (Fig. 3A, B). Nest boxes selected by House Sparrows were located in open grassy habitat as indicated by projections on component I (Fig. 3C). However, no other strong patterns were discernable with respect to variables summarized by components II and III (Fig. 3C, D). The unoccupied plots

Table 2

Prinicipal-component Loadings and Results of Principal-components Analysis Based on 40 Vegetational Variables[a]

Variable	Component I	Component II	Component III	Variable	Component I	Component II	Component III
1 OAKA	0.394	−0.280	0.379	21 STEMV	0.268	0.167	−0.197
2 OAKB	**0.605**	0.070	**0.420**	22 WOODYCOV	0.420	−0.032	0.068
3 OAKC	0.165	−0.087	0.176	23 FORBCOV	0.463	0.340	−0.083
4 NONA	0.560	0.412	−0.201	24 GRASSCOV	**−0.818**	−0.229	−0.130
5 NONB	0.407	0.437	−0.009	25 LEAFCOV	**0.669**	0.060	0.196
6 NONC	−0.071	0.286	−0.114	26 ROCKCOV	0.003	0.149	0.015
7 JUNA	0.501	−0.315	**−0.415**	27 BARECOV	0.203	0.176	0.337
8 DENSO	0.373	−0.335	**0.671**	28 HITSA	0.398	0.011	−0.102
9 DENSN	−0.020	**0.741**	−0.305	29 HITSB	0.527	−0.200	−0.187
10 DENSJ	−0.053	−0.492	**−0.420**	30 HITSC	0.573	−0.345	−0.367
11 BAOAK	**0.762**	−0.128	**0.481**	31 HITSD	0.588	−0.354	−0.366
12 BANON	0.547	**0.635**	−0.189	32 HITSE	**0.641**	−0.312	−0.385
13 BAJUN	0.498	−0.389	**−0.517**	33 HITSF	**0.725**	−0.201	−0.279
14 RDOAK	0.516	−0.369	**0.648**	34 HITSG	**0.700**	−0.146	−0.170
15 RDNON	−0.131	**0.747**	−0.362	35 HITSH	**0.809**	−0.026	−0.149
16 RDJUN	−0.148	−0.459	**−0.440**	36 HITSI	**0.783**	0.128	0.060
17 VARQUAD	0.583	−0.103	−0.127	37 HITSJ	**0.750**	0.281	0.131
18 STEMO	0.387	−0.413	0.314	38 HITSK	**0.709**	0.302	0.173
19 STEMN	0.399	0.217	−0.273	39 CANHT	**0.839**	0.275	0.162
20 STEMJ	0.491	−0.234	**−0.439**	40 VARCAN	**0.840**	0.174	0.042

[a] Relatively high loadings highlighted in bold as follows: (component I) > |0.6|; (component II) > |0.5|; (component III) > |0.4|.

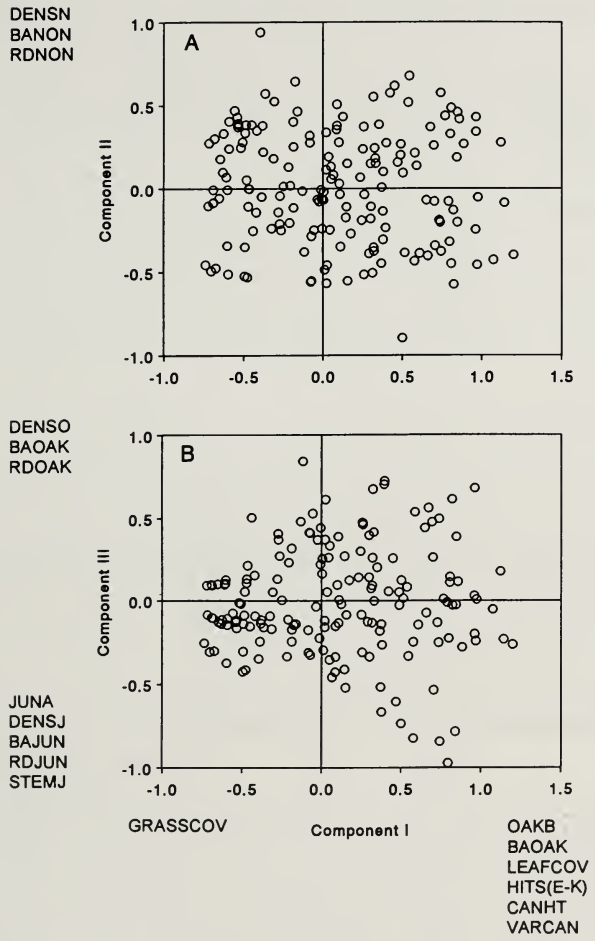

FIG. 1. Projections of all 194 sample plots (for five species and for unoccupied sites) onto principal components based on 40 vegetation variables: (A) components I and II; (B) components I and III. Codes indicated for variables with high positive or negative loadings on particular axes.

were broadly distributed on all three principal-component axes (Fig. 3E, F). Since the study areas were "saturated" with nest boxes, it is not unexpected that projections of unoccupied plots were distributed through a variety of habitats.

Measures of reproductive success were calculated (i.e., percent fledged from eggs laid and percent fledged from eggs hatched) and analyzed with respect to projections onto components I, II, and III for all occupied nest

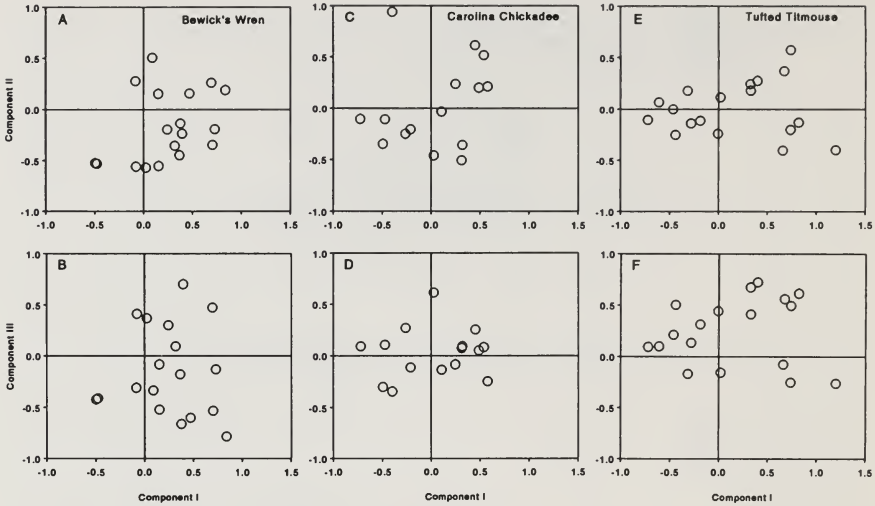

FIG. 2. Projections for (A–B) Bewick's Wrens, (C–D) Carolina Chickadees, and (E–F) Tufted Titmice onto principal components I, II, and III resulting from analysis of all 194 sample plots and 40 vegetation variables.

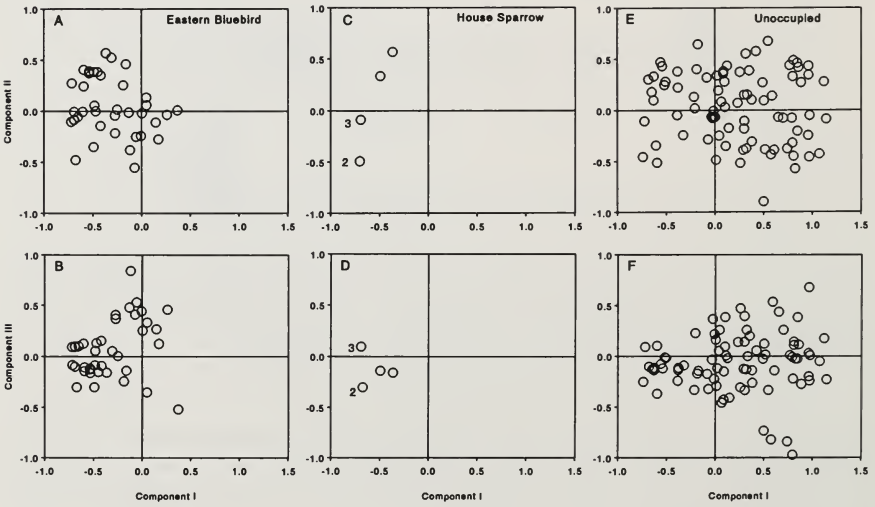

FIG. 3. Projections for (A–B) Eastern Bluebirds, (C–D) House Sparrows, and (E–F) unoccupied plots onto principal components I, II, and III resulting from analysis of all 194 sample plots and 40 vegetation variables. Numbers in panels C and D denote placement of an indicated number of overlapping points.

boxes. Reproductive success exhibited no correlation with component projections for any of the five species.

Niche overlap and breadth.—Our analyses of niche overlap and breadth involve the distributions of nests of particular species along principal-component I (Fig. 4), which is a composite vegetation measure with low values indicating open habitats and high values indicating relatively dense woodland. The 194 nest boxes were placed in nine categories based on their projections onto principal component I. As indicated by the forward-most graph in Fig. 4, the boxes were distributed relatively uniformly along the first principal component, with a slightly greater proportion occurring at the open end of the spectrum and slightly fewer at the woodland end.

The 18 Bewick's Wren nests were distributed over much of the component's range, although the wrens did not use boxes in the most open habitat or in the dense woodland (Fig. 4; see also Fig. 2A). The 15 Carolina Chickadee nests also were found along much of the gradient, although the species did not use boxes in the two categories representing the densest woodland available (Fig. 2C). The 19 nests of the Tufted Titmice were nearly uniformly distributed along the habitat gradient, while the 50 Eastern Bluebird nests were found in more open areas, with almost half occurring in nest boxes in the category representing the open extreme of the habitat gradient (Fig. 3A). All of the nine House Sparrow nests were in boxes in the two categories including nest boxes placed in the most open areas (Fig. 3C).

Niche-overlap values using the simplified Morisita index ranged from 0.058 for the Bewick's Wren and House Sparrow to 0.866 for the Eastern Bluebird and House Sparrow (top of Table 3; species ordered on the basis of number of nests found). As indicated in the Methods, when sampling without replacement, the expected overlap values are higher for species where one or both had a relatively large number of nests. Thus, the expected values (see simulation means in middle of Table 3) range from 0.645 for the Carolina Chickadee and House Sparrow to 0.812 for the Eastern Bluebird and Tufted Titmouse.

Statistically significant negative deviations (bottom section of Table 3), which indicate less overlap than predicted on the basis of chance alone, were found for House Sparrow (graph 5 in Fig. 4) with the Carolina Chickadee, Bewick's Wren, and Tufted Titmouse (graphs 1–3 in Fig. 4). This is particularly marked for the comparison with the Bewick's Wren, a species not found nesting in the most open areas (see far left of graph 1 in Fig. 4). A similar pattern of significant negative deviations was found for the Eastern Bluebird (graph 4 in Fig. 4) with the Carolina Chickadee, Bewick's Wren, and Tufted Titmouse (bottom line in Table 3). Not sur-

TABLE 3

NICHE OVERLAP BETWEEN SPECIES PAIRS AS INDICATED BY SIMPLIFIED MORISITA INDEX. ACTUAL VALUE, MEAN VALUE FOR 1000 SIMULATIONS USING SAME SAMPLE SIZES, AND DEVIATION OF SIMULATED FROM ACTUAL[a,b]

Species	House Sparrow	Carolina Chickadee	Bewick's Wren	Tufted Titmouse
		Actual overlap (M)		
Carolina Chickadee	0.230			
Bewick's Wren	0.058	0.800		
Tufted Titmouse	0.400	0.706	0.702	
Eastern Bluebird	0.866	0.425	0.250	0.617
		Simulated overlap ($\bar{M}_s$)		
Carolina Chickadee	0.645			
Bewick's Wren	0.656	0.720		
Tufted Titmouse	0.655	0.731	0.743	
Eastern Bluebird	0.706	0.782	0.809	0.812
		Deviation ($M - \bar{M}_s$)		
Carolina Chickadee	−0.414**			
Bewick's Wren	−0.598***	0.080 ns		
Tufted Titmouse	−0.255*	−0.025 ns	−0.041 ns	
Eastern Bluebird	0.160*	−0.357**	−0.559***	−0.195*

[a] Species arranged by sample size: House Sparrow (9), Carolina Chickadee (15), Bewick's Wren (18), Tufted Titmouse (19), and Eastern Bluebird (50).

[b] ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

prisingly, there is a significant positive deviation in the overlap value for the Eastern Bluebird and House Sparrow (Table 3; graphs 4 and 5 of Fig. 4), indicating that they are more likely to be found together in the same habitat (i.e., open areas) than expected by chance. The habitat-overlap values involving all pairs of three species (i.e., Carolina Chickadee, Bewick's Wren, and Tufted Titmouse) do not deviate significantly from values expected simply by chance (bottom section of Table 3).

For niche breadth, the calculated Smith index (B) ranged from 0.596 for the House Sparrow to 0.937 for the Tufted Titmouse (Table 4). The species in Table 4 have been ordered on the basis of the number of nests and, as indicated by the mean simulated values ($\bar{B}_s$), the niche breadth value increases as the sample increases, since sampling is done without replacement. For three species, the negative deviations from expected values were statistically significant (Table 4). The House Sparrow and Eastern Bluebird were restricted to the open habitats, while Bewick's Wrens more often nested in semiopen areas (Fig. 4) than predicted by chance. For the Carolina Chickadee and Tufted Titmouse, nest-box use

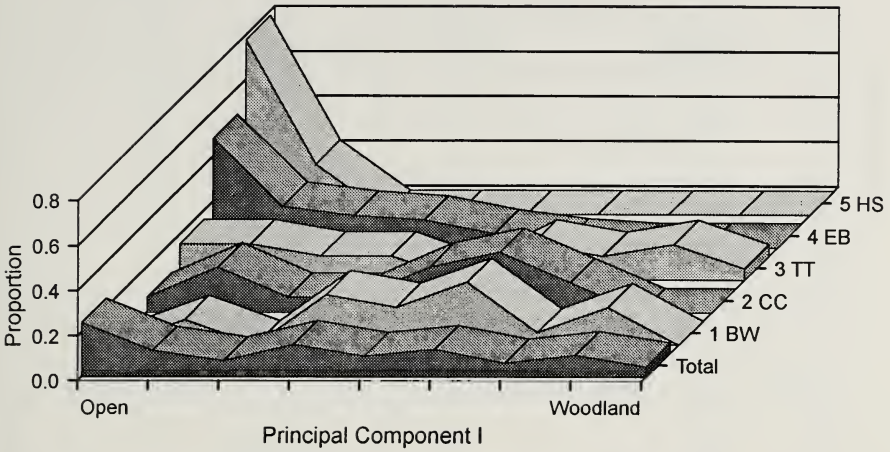

FIG. 4. Groupings of projections onto principal component I for each species into nine categories, with proportions in each group for each species indicated. Proportions of all nest boxes (194 total) in each category denoted in foremost graph.

relative to this habitat gradient was not different from random expectations.

Discriminant analysis.—Canonical variables provided separation of nest sites occupied by the different species (Fig. 5). Each plot was assigned to one species using classification functions developed in the stepwise discriminant analysis (top of Table 5). The greatest accuracy with respect to correctly classifying a given nest as having been used by a particular species was achieved for plots occupied by Eastern Bluebirds, with 70.0% correctly classified (Table 6). Approximately one-half of the plots occupied by Bewick's Wrens and Carolina Chickadees were clas-

TABLE 4

NICHE BREADTH AS INDICATED BY SMITH INDEX[a]

Species	No. nests	B	B_s	$B - B_s$[b]
House Sparrow	9	0.596	0.806	−0.210**
Carolina Chickadee	15	0.857	0.890	−0.033 ns
Bewick's Wren	18	0.790	0.910	−0.120**
Tufted Titmouse	19	0.937	0.919	0.018 ns
Eastern Bluebird	50	0.844	0.982	−0.138***

[a] Actual value (B), mean value (B_s) for 1000 simulations using same sample size, and deviation of simulated from actual ($B - B_s$).

[b] ns, $P > 0.05$, **, $P < 0.01$, ***, $P < 0.001$.

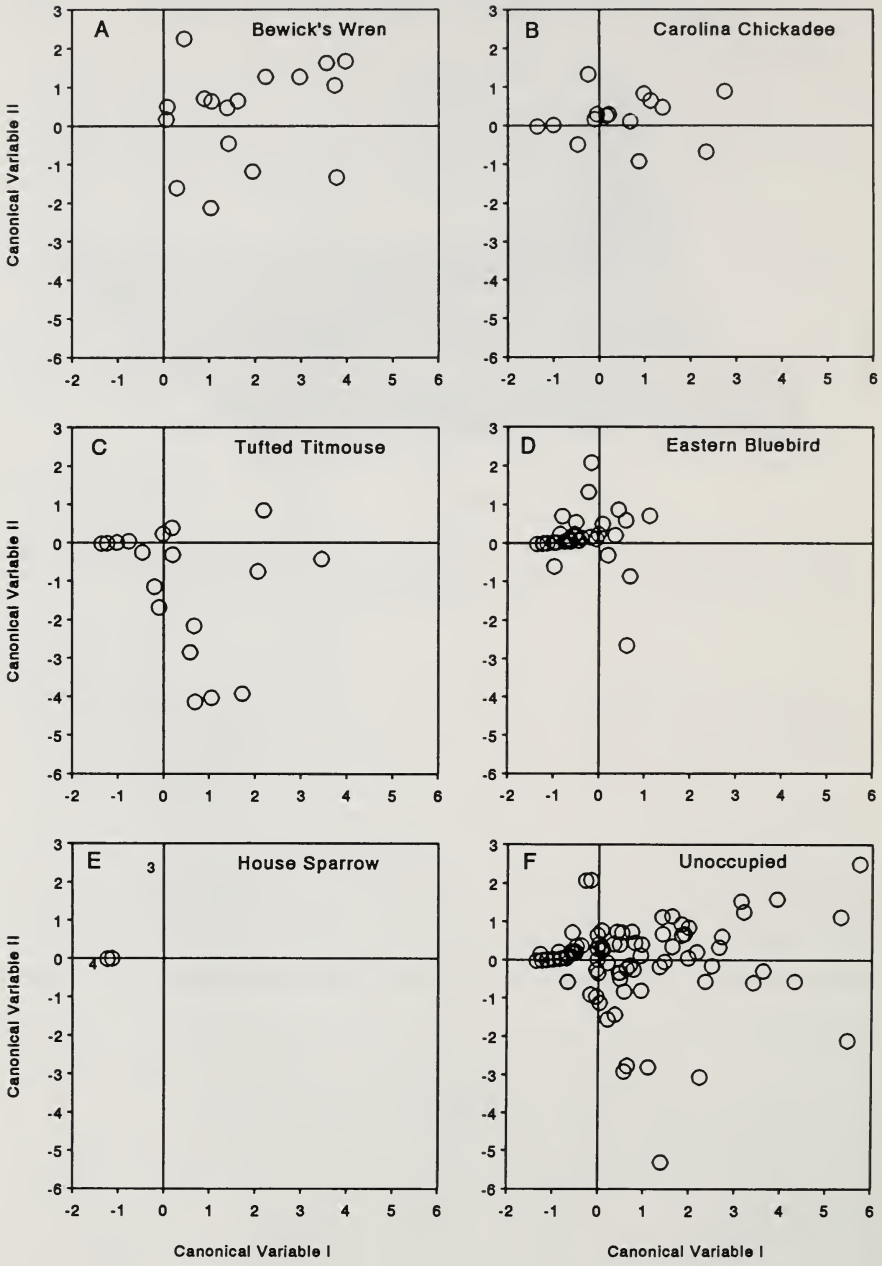

FIG. 5. Projections of sample plots for each species and unoccupied plots on canonical variables I and II: (A) Bewick's Wren; (B) Carolina Chickadee; (C) Tufted Titmouse; (D) Eastern Bluebird; (E) House Sparrow; (F) unoccupied plots. Numbers in panel E denote placement of an indicated number of overlapping points.

TABLE 5

STATISTICS FOR STEPWISE DISCRIMINANT ANALYSES OF PLOTS

Variable	*F*-value to enter	Order of entry	Standardized canonical-variable coefficients				Classification function[1]				
			1	2	3	4	BW	CC	TT	EB	HS
All species											
HITSD	15.92	1	0.343	−0.818	−0.458	−0.167	0.996	0.209	0.252	0.013	−0.050
OAKB	8.39	2	0.218	0.475	−0.618	−0.592	0.552	0.157	1.132	0.054	0.044
VARQUAD	4.79	3	0.704	0.191	−0.267	0.701	0.858	1.112	0.258	0.438	0.157
DENSJ	4.08	4	0.413	0.040	0.760	−0.592	3.246	1.611	0.873	0.778	4.048
Constant			−1.347	−0.026	−0.193	0.641	−6.518	−4.184	−3.824	−1.978	−2.708
All species except House Sparrow											
HITSD	17.95	1	0.748	0.184	0.709	—	0.923	0.193	0.233	0.012	—
OAKB	9.67	2	0.347	−0.949	0.009	—	0.456	0.118	1.031	0.037	—
VARQUAD	4.78	3	0.388	0.282	−0.936	—	0.806	1.039	0.546	0.409	—
Constant			−1.279	0.005	0.668	—	−5.302	−3.623	−3.391	−1.693	—

[1] Species codes: BW, Bewick's Wren; CC, Carolina Chickadee; TT, Tufted Titmouse; EB, Eastern Bluebird; HS, House Sparrow. Tabulated values used with original values for variable Products of corresponding measurements and function values summed and then added to constant. Plot classified into particular group based on which classification function produces th highest value.

TABLE 6

CLASSIFICATION OF PLOTS USING STEPWISE DISCRIMINANT ANALYSIS[a]

Group	Percent correctly classified	Classified as				
		BW	CC	TT	EB	HS
		All plots				
Bewick's Wren (BW)	55.6	10	4	2	0	2
Carolina Chickadee (CC)	53.3	3	8	0	3	1
Tufted Titmouse (TT)	36.8	3	2	7	7	0
Eastern Bluebird (EB)	70.0	3	7	2	35	3
House Sparrow (HS)	33.3	0	0	0	6	3
Unoccupied plots	—	23	19	13	25	3
		All species except House Sparrow				
Bewick's Wren	50.0	9	5	2	2	—
Carolina Chickadee	60.0	2	9	0	4	—
Tufted Titmouse	36.8	3	3	7	6	—
Eastern Bluebird	74.0	2	9	2	37	—
House Sparrow[b]	—	0	0	0	9	—
Unoccupied plots	—	26	18	12	27	—

[a] Standard classification and jackknife classification were the same.

[b] For this analysis, House Sparrow plots not used in canonical-variates analysis, but then classified *a posteriori* into one of the other species.

sified correctly (55.6 and 53.3%, respectively). However, only one-third of Tufted Titmouse and House Sparrow plots were correctly assigned (36.8 and 33.3%, respectively). The unoccupied plots also were classified by the functions derived from stepwise discriminant analysis. All species were evenly represented by the classification of unoccupied plots with the exception of the House Sparrow. Only three of the unoccupied plots were classified as being typical for House Sparrows (Table 6).

Stepwise discriminant analysis was repeated, with plots occupied by House Sparrows entered as unknowns to determine if classification accuracy for plots was affected by the inclusion of House Sparrow plots. The resulting classification function is given in Table 5 (bottom). This analysis provides information on the potential effects of an introduced species on nest-site selection of native species. All plots including those occupied by House Sparrows were classified into the remaining four species groups. As in the previous analysis, the greatest classification accuracy was attained for plots occupied by Eastern Bluebirds, with 74.0% correctly classified (bottom of Table 6), 4% higher than when House Sparrow plots were included in a separate group. Classification accuracy also increased for plots used by Carolina Chickadees, with 60.0% correctly classified. The percentage of Tufted Titmouse plots correctly clas-

sified remained the same (36.8%). Correct classification of plots occupied by Bewick's Wrens decreased 5.6% to 50.0%. All of the plots used by House Sparrows were assigned as Eastern Bluebird plots (bottom of Table 6). The unoccupied plots were assigned to species groups, with 32.5% of plots identified as Eastern Bluebird plots and 14.5% identified as Tufted Titmouse plots. The modest increases in classification accuracy reflect the overlap of habitat preferences.

In both discriminant analyses, the number of decimeters with tree hits in the >1.5–2.0-m height zone (HITSD), the number of oaks with dbh >22.5–52.5 cm (OAKB), and the standard deviation of the number of trees per quadrant (VARQUAD) were the first three variables entered (Table 5). The first analysis, which involved all groups, also included the density of junipers (DENSJ) as the fourth variable. Thus, the vegetation at lower heights (HITSD, DENSJ) and vegetation density (VARQUAD, DENSJ) are, in combination, the most useful nesting-habitat characteristics to distinguish among these five secondary cavity-nesting species.

DISCUSSION

Species preferences.—The general vegetational gradients calculated in our study were quite similar to those obtained by James (1971) in an evaluation of Arkansas breeding birds. Component I in both studies represented a gradient from open grassy areas to wooded areas. Our component III reflects a strong gradient from decreasing junipers to increasing oaks. Although junipers were not separated from other trees in variables used in the Arkansas study, the compact shape of junipers is reflected structurally by the dense shrubs represented on component II of the James study, which was a gradient from dense shrubs to medium-sized trees and few shrubs.

Results from stepwise discriminant analysis in the Arkansas study indicated that the discriminant axes represented a continuum from open country to forest associations, and one from upland to bottomland areas (James 1971). Carolina Chickadees and Tufted Titmice exhibited high values on the discriminant axis, indicating their strong association with wooded areas. These results differ somewhat from our findings in that Carolina Chickadee plots in our study areas primarily were located in areas with scattered trees. In our study, Tufted Titmice nests were not restricted to heavily wooded areas, but also were found in open areas with few trees. Bent (1946) described the general breeding habitat of chickadees and titmice as being the forest edge, but noted that Tufted Titmice occasionally nest along borders of fields and in open pastures. The niche-breadth index we calculated also indicates that titmice exhibit a broad range of habitat use.

Posey (1974), characterizing the habitats of breeding birds in Ozark shrubby old fields, demonstrated vegetational patterns similar to those found in our study. He evaluated 16 vegetational characters to describe the structural features of avian breeding habitats, using as focal points the song-perch sites. From principal-components analysis, he found that component I represented a vegetational biomass gradient (i.e., a gradient from open grassy fields to shrubby wooded areas). Component III showed strong correlations with shrub density and canopy variables, indicating a gradient from dense shrubs to wooded areas with little understory. Among the species evaluated, Posey (1974) found that Eastern Bluebird plots had low values on component I, indicating the strong preference of this species for open grassy areas. Eastern Bluebird nest sites described in our study also suggest that the species has a strong preference for open grassy areas. Our simulation results indicate Eastern Bluebirds have a relatively narrow niche breadth. For this species, habitat characteristics of song-perch sites (Posey 1974) and nest-box sites (our study) were very similar. Several studies (e.g., Bent 1949; Zeleny 1976; Pinkowski 1976, 1977, 1978) also have shown that breeding Eastern Bluebirds prefer forest edges and open areas with scattered trees. Willner et al. (1983) noted that bluebirds selected nest sites in areas of poor soils where herbaceous vegetation was sparse or where mowing had recently occurred.

Whitmore's (1975) habitat-ordination study of passerine birds of the Virgin River Valley in southwestern Utah incorporated discriminant-function analyses to determine the most important characters that, in combination, would distinguish among species. As with most other avian habitat-ordination studies, he found that the first discriminant axis represented a gradient from low canopy cover to densely forested areas. Among the species evaluated, Bewick's Wrens were located midway along the discriminant axis; they showed a preference for relatively open areas interspersed with trees. In our study, Bewick's Wren plots were more closely associated with wooded areas containing junipers. Bent (1948) indicated that, although the Bewick's Wren is found in a variety of habitats (including open woodlands, upland thickets and fence rows), the nests often are well concealed (e.g., in the center of dense brush). A possible explanation for the differences in habitat characteristics shown for perch sites (Whitmore 1975) and nest sites (our study) is that the female selects areas with more vegetation near the nest site to provide protection and to make the nest relatively inconspicuous. However, the song-perch sites, located by singing males, are in more open areas, which provide increased visibility for (and of) displaying males.

Conner et al. (1983) used principal-components and discriminant analyses to ordinate breeding habitat of bird species on vegetational continua

in eastern Texas. They found Tufted Titmice most often in wooded areas and those with relatively large numbers of shrubs. Carolina Chickadees were also closely associated with wooded areas, but preferred open understories. In our study, Carolina Chickadees preferred areas that were relatively open with scattered trees, and Tufted Titmouse plots were broadly distributed showing no particular association with open or wooded areas.

Interspecific competition.—Native species are not only influenced by human disturbances, but by introduced species such as the House Sparrow and European Starling (*Sturnus vulgaris*). Since their introduction, these species have invaded much of North America (Zeleny 1976). Cavity nesters are particularly vulnerable to the aggressive nature of these species, which may compete for available nest sites. European Starlings did not affect birds using our nest boxes, because the entrance hole was too small for starlings to enter. However, House Sparrows were not prevented from usurping nest boxes. The native species most affected by House Sparrows in our study appears to be the Eastern Bluebird. As illustrated in one of the stepwise discriminant analyses (bottom of Table 6), all plots occupied by House Sparrows were classified as Eastern Bluebird plots, indicating the similarities between nest sites of these two species. In addition, simulation results showed substantial overlap for House Sparrows and Eastern Bluebirds. Willner et al. (1983) investigated nest-box use and habitat characteristics in Maryland employing an alternate set of environmental variables. Using discriminant functions, they found that five of six nest boxes occupied by House Sparrows were in habitats favored by bluebirds.

In our study, seven of nine nest boxes used by House Sparrows were initially occupied by Eastern Bluebirds. In addition, we have direct evidence of competition occurring between the two species with Eastern Bluebirds being detrimentally affected. On 14 May and 25 May 1990, a House Sparrow was observed displacing a male Eastern Bluebird. In both cases a male bluebird was found dead in the nest box on the following day (Pogue, pers. obs.). Carter (1981), conducting studies in the same area of Oklahoma, also found that House Sparrows displaced bluebirds during nesting, and Zeleny (1976) noted that House Sparrows are exceptionally aggressive and usually can displace bluebirds from a particular site. Although the Eastern Bluebird population has increased over most of its range in recent years (Sauer and Droege 1990), continued growth of the House Sparrow population in rural areas could negatively affect Eastern Bluebird populations due to the similarity of nest sites selected by the two species and the aggressive nature of House Sparrows.

Characteristics of simulation approach used.—The niche-breadth and overlap simulations were helpful in comparing and contrasting species. These analyses support the suggestion that nest-box use by House Sparrows and Eastern Bluebirds is significantly more similar than expected by chance. This point was demonstrable in spite of the relatively limited number of House Sparrow pairs using nest boxes in the study areas. Not surprisingly the simulations also showed House Sparrows and Eastern Bluebirds to be markedly different from the other three species in their choice of nest boxes along the general gradient summarizing the degree of habitat openness.

Simulations by their very nature have limitations. When initiating such an analysis, it is necessary to make decisions concerning the extent to which a simulation model should directly reflect nature. Often there is a trade-off involving generality versus closeness of fit to a particular situation. We based habitat categories on the projections of nest boxes onto principal component I and, thus, confined the analysis to those habitat characteristics summarized by this component. A more elaborate simulation involving groups based on more components likely would have shown the Bewick's Wren to have less habitat overlap with the Tufted Titmouse and Carolina Chickadee, since the overall principal-component analysis indicated that the wren has an affinity for areas with junipers (relevant characteristics summarized on principal component III). At the same time, detailing more habitat aspects in the simulation could have obscured the extent to which overlap is evident when one focuses on the degree of habitat openness. We made the conscious decision to analyze only component I because it represented an important and general habitat descriptor—a readily understandable dimension worthy of special attention because it summarizes a basic continuum separating habitats of the region.

Two other aspects of our simulation model deserve comment. First, we deliberately sampled without replacement when establishing an expected distribution across habitats for a given species. Even though not all nest boxes were occupied, only a certain number were available (just as only a finite number of natural cavities exist in a particular area). Since nest boxes represented a limited resource, this seemed to be the most appropriate approach. In terms of the number of nest boxes potentially available to a particular species or a particular pair, our model was not totally realistic since the birds and nest boxes in the field were evaluated over two seasons, while we set up the simulation as if a single season were involved; given the clear-cut simulation results we do not believe that this simplification detracts from the general findings.

Second, our simulations (and the measures of niche overlap and

breadth) were based on discrete, unordered habitat categories, while in fact the nine groupings can be ordered (i.e., they represent portions of a subdivided continuum). The main effect of using unordered categories probably was to make statistical tests somewhat more conservative than would have been the case if ordered categories had been employed (along with appropriate coefficients); with ordering, a coefficient would take into account the fact that species tended to have similar frequencies in adjacent habitat categories. Additional simulations with more elaborate assumptions could be helpful in further elucidating habitat relationships of these birds. The simulations reported here were useful in clarifying interspecific associations and helping us to understand the expected values for niche breadth and overlap given a limited resource (i.e., nest boxes).

Concluding remarks.—The quantitative findings obtained through our analyses reflect the general qualitative descriptions in the literature of breeding habitats for these secondary cavity-nesting species. For example, breeding sites of Bewick's Wrens are generally described as being located in brushy areas along the forest edge (Bent 1948). Carolina Chickadees and Tufted Titmice are associated with deciduous and mixed deciduous-juniper woodlands (Ehrlich et al. 1988); however, as pointed out earlier, Bent (1946) noted that the Tufted Titmouse sometimes nests along borders of fields and in open pastures. Zeleny (1976) indicated that Eastern Bluebirds prefer breeding sites in open country with scattered trees and forest edge. House Sparrow breeding sites are most often located near human habitation; however, in rural areas, House Sparrows select nest sites in any available cavity, including nest boxes (Summers-Smith 1963).

Overall, for our analyses, nest sites of the species studied can be characterized on a gradient, with Bewick's Wrens preferring nest sites in wooded areas containing junipers, and Carolina Chickadees selecting areas mixed with junipers and oak trees. Tufted Titmice selected nest sites in both open and wooded areas; however, plots found in wooded areas that were used by Tufted Titmice contained few junipers and deciduous trees other than oaks. Eastern Bluebirds and House Sparrows preferred sites in open grassy areas with few trees.

Clearly, our investigation and those of others indicate marked differences in habitat preferences of cavity-nesting species. For a nongame manager wanting to accommodate particular cavity-nesting species, nest boxes should be placed within the appropriate interval along the main habitat gradient. Zeleny (1976) noted that nest boxes in habitat suitable for Eastern Bluebirds but placed relatively near buildings would, not surprisingly, have a greater probability of attracting House Sparrows. For Eastern Bluebirds and House Sparrows, our data indicate that there are virtually no differences in the habitat characteristics of nest boxes select-

ed, a conclusion also reached by Willner et al. (1983). It is evident that these two species prefer very similar sites.

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INFLUENCE OF NEST-SITE COMPETITION BETWEEN EUROPEAN STARLINGS AND WOODPECKERS

Danny J. Ingold[1]

Abstract.—I studied the nesting behavior of 40 pairs of Red-bellied Woodpeckers (*Melanerpes carolinus*), 42 pairs of Northern Flickers (*Colaptes auratus*), and 23 pairs of Red-headed Woodpeckers (*M. erythrocephalus*) during three breeding seasons, 1990–1992, in east-central Ohio. European Starlings (*Sturnus vulgaris*) and Red-bellied Woodpeckers initiated nesting at the same time in early April, whereas flickers began nest excavation in late April and Red-headed Woodpeckers in early May. Red-bellied Woodpeckers incurred the brunt of starling competition for freshly excavated nest cavities and lost 39% of their cavities to starlings. Flickers and Red-headed Woodpeckers were significantly more aggressive than Red-bellied Woodpeckers when defending their nest cavities. Fourteen percent of flicker cavities and 15% of Red-headed Woodpecker cavities were usurped by starlings. Numbers of starling interactions with both Red-bellied and Red-headed woodpeckers decreased significantly ($P < 0.05$) over the breeding season. Woodpecker pairs unable to avoid starling competition may not have suffered reductions in fecundity since at least some of these pairs were able to renest successfully later in the season. *Received 19 July 1993, accepted 21 Sept. 1993.*

The availability of suitable nest cavities and sites for nest cavities (i.e., dead limbs and snags) limits the reproductive success of hole-nesting birds (Cline et al. 1980, Mannan et al. 1980, Stauffer and Best 1982, Nilsson 1984, Raphael and White 1984, Cody 1985, Li and Martin 1991). The European Starling (*Sturnus vulgaris*), an introduced secondary cavity-nesting species, is known to compete with a variety of native North American primary and secondary cavity nesters for nest sites (Howell 1943, Kilham 1958, Polder 1963, Zeleny 1969, Reller 1972, Jackson 1976, Short 1979, Ingold and Ingold 1984, Weitzel 1988). However, surprisingly few studies have been conducted in order to determine whether woodpeckers or other cavity nesters actually suffer reductions in fecundity as a result of starling harassment (see van Balen et al. 1982, Nilsson 1984). Ingold (1989a) found that Red-bellied Woodpeckers (*Melanerpes carolinus*) suffered significant reductions in their reproductive success when competing with starlings, but Red-headed Woodpeckers (*M. erythrocephalus*) did not. Kerpez and Smith (1990) found that significantly fewer Gila Woodpeckers (*M. uropygialis*) nested in areas of starling overlap vs areas where starlings were absent; however, they were unable to detect a similar trend in Northern Flickers (*Colaptes auratus*). Troetschler (1976) concluded that Acorn Woodpeckers (*M. formicivorus*) nesting in the presence of starlings were not adversely affected since they were able

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to excavate new nest cavities or successfully delay nesting until later in the season. Thus, although starlings interact with several cavity-nesting species for nest sites, they may not reduce the reproductive success of all of them.

Red-bellied and Red-headed woodpeckers and Northern Flickers are common primary cavity-nesting species whose ranges are broadly sympatric with European Starlings in eastern North America. In Ohio, Red-bellied Woodpeckers (RBW) are locally common permanent residents, while flickers are common to abundant summer residents (Peterjohn and Rice 1991). Red-headed Woodpeckers (RHW), however, are considered uncommon in the Unglaciated Plateau region of southeastern Ohio (Peterjohn and Rice 1991). European Starlings are abundant permanent residents throughout the state. Although all three woodpecker species occupy slightly different niches (Conner and Adkisson 1977, Stauffer and Best 1982), they all have been reported to lose nest cavities to starlings (Bent 1939, Reller 1972, Kilham 1983, Ingold 1989a), and occasionally to other woodpecker species (Bent 1939, Nichols and Jackson 1987, Ingold 1989b). Moreover, since RBWs in Ohio initiate nest construction in early April at the same time as starlings (Trautman 1940, Peterjohn 1989), they could be more vulnerable to starling harassment than other woodpeckers.

I quantified the nesting phenology of these four species and identified the degree of phenological overlap among them. I also attempted to determine whether a correlation exists between the aggressive nature of each woodpecker species and its ability to defend its nest cavities against starlings and other woodpeckers. I discuss whether any of these woodpecker species is suffering reductions in fecundity as a result of harassment by starlings.

STUDY AREA AND METHODS

From the last week of March through the last week of August 1990–1992, I located active woodpecker and starling nest cavities on the Muskingum College campus in the city of New Concord and on several agricultural areas near New Concord. The study area covers about 1000 ha in Muskingum and Guernsey Counties and constitutes a variety of habitats. The campus and city are characterized by a variety of hardwood species dominated by maples (*Acer* spp.), surrounded by lawns, houses, buildings, and streets. The agricultural sites consist primarily of pastures used primarily for grazing, with occasional planted fields, streams, scattered hardwoods, and snags. At several locations, patches of trees from 0.25 ha to ca 5 ha border pastures and cropland. These woody patches are dominated by black locusts (*Robinia pseudoacacia*), American sycamores (*Plantanus occidentalis*), beeches (*Fagus grandifolia*), oaks (*Quercus* spp.), and maples.

Since starlings and RBWs initiated nesting at the same time, RBW pairs were categorized as either competitors or controls (competition free). Pairs were considered controls if I did not detect starlings in a 0.25 circular ha around their nest site throughout the nesting season (cf Ingold 1989a). Although this method of categorization is somewhat arbitrary and does

not preclude possible contact between some control woodpeckers and starlings, this criterion is fairly rigorous and makes it unlikely.

I monitored each active woodpecker and starling nest for a minimum of 30 min once a week between 07:00 and 18:00 h DST to determine the status and detect possible starling/woodpecker and interspecific woodpecker interactions. I observed woodpecker cavities where starlings or other woodpecker species were present up to 3 h/week. Interactions were considered to occur when the individuals involved acknowledged each other's presence. Such acknowledgments included vocalizations, pursuit flights, or physical confrontations at the nest cavity (cf Ingold 1989a). I quantified all interactions, noting the aggressor and subordinate in each. Each week I climbed to those cavities that could be reached to confirm occupancy and nest status. Nest contents were examined with a light and mirror. In order to facilitate individual recognition of the woodpeckers, I captured and color-banded as many adults and nestlings as possible throughout the study.

I used Kolmogorov-Smirnov tests to determine whether differences existed in the timing of nest construction, incubation, and the presence of nestlings and fledglings in starlings, RBWs, and flickers among years (thus 12 tests were conducted on each species). Eleven of 12 tests on starlings were not significant ($P > 0.05$), while 10 of 12 tests on RBWs and flickers were not significant ($P > 0.05$). For this reason, and because my sample sizes are small (N = 17, 16, and 12 starling pairs; 9, 16, and 15 RBW pairs; and 13, 16, and 14 flicker pairs from 1990–1992 respectively), I pooled the data in all three species. The sample size of RHWs was particularly small (N = 9, 7, and 7 pairs), and I did not perform Kolmogorov-Smirnov tests. Rather, I pooled these data as well.

Since the number of interactions per/wk among starlings and woodpeckers was small and sample sizes were unequal, I tested for differences among them for the three-year period using a Kruskal-Wallis test. No differences were detected ($P > 0.05$) and these data were pooled. Numbers of woodpecker cavity usurpations by starlings were small, and the percentage of cavities usurped relative to the number of cavities available differed only minimally between years. These data were, therefore, pooled.

RESULTS

Nesting phenology.—Nest starts by starlings and RBWs occurred in late March and early April of all three years (Fig. 1). By the end of April, at least 75% of all active RBW nests were still being excavated, while 80% of the starling nests were in the incubation stage. Flickers initiated nest excavation about 10 days after RBWs in mid-April, and RHWs began excavating the first week of May (Fig. 1). Consequently, these species avoided the intense starling harassment that RBWs incurred in early April. Starling clutch starts, nests with nestlings, and nests with fledglings followed a bimodal pattern similar to that reported by Ingold (1989a) and Dakin (1984) in Mississippi (Figs. 2, 3, 4), suggesting that several pairs had two broods or attempted second nests after unsuccessful first nesting attempts. The incubation, nestling, and fledgling periods for RBWs, and to a lesser extent flickers, overlap with starlings, while RHWs are about two weeks behind in all phases (Figs. 2, 3, 4). The nesting period of starlings extended into mid-July (Fig. 4), and at least 38% of all pairs successfully reared two broods. Flickers fledged young through late July,

while RBWs and RHWs had active nests into August (Fig. 4). Only one woodpecker pair (RHW) was known to attempt a second brood after successfully completing a first one.

Of 40 RBW pairs observed, 12 nested in the absence of starlings. At least seven of these pairs (58%) were incubating eggs by late April, compared to only 4% of pairs competing with starlings. The proportion of competition-free RBW pairs with eggs before 15 May was significantly greater than for competing pairs with eggs before this date ($\chi^2 = 12.7$, df $= 1$, $P < 0.001$). In addition, the proportion of control RBW pairs with nestlings before 1 June was significantly greater than for competing pairs with nestlings before this date ($\chi^2 = 9.87$, df $= 1$, $P < 0.01$). I was unable to climb to enough woodpecker cavities to determine whether or not any significant trends existed in clutch sizes, numbers of nestlings, and/or fledglings of competing versus control pairs.

Interactions.—Nesting starlings were common on all study sites except densely forested patches and were particularly abundant in town. Conversely, 96% of all woodpecker pairs nested on agricultural and forested areas outside town. Thus, although competitive interactions among starlings and woodpeckers were frequent, at least 95% of them occurred on the rural study sites.

I observed a total of 41 interactions between starlings and RBWs, all near freshly excavated RBW cavities. Twenty-nine of these (71%) occurred during April when both species were initiating nest efforts. Regression analysis reveals a significant negative correlation between the number of starling/RBW interactions and the progression of time during the nesting season ($F = 10.96$, df $= 1,13$; $P < 0.01$; Fig. 5). Seventeen of 25 (68%) starling/RHW interactions occurred during May when RHW were initiating nest efforts. The number of these interactions was also negatively associated with the progression of time ($F = 5.46$, df $= 1,11$; $P < 0.05$; Fig. 5). No definite pattern exists for starling/flicker interactions; however, most occurred during the first week of June when many flicker pairs were incubating and several starling pairs were beginning second nest efforts.

There were striking differences in the aggressive behavior of these species (Table 1). Starlings and RHWs were about equally aggressive, and both were significantly more aggressive than RBWs and flickers (contingency table Chi-square tests, $P < 0.01$); moreover, flickers were significantly more aggressive than RBWs (contingency table Chi-square test, $P < 0.05$) (Table 1).

Cavity usurpations.—Of 54 freshly excavated RBW nest cavities, 21 (39%) were usurped by starlings, thirteen during April when both species were initiating nesting (Fig. 6). Starling usurpations of RBW cavities were

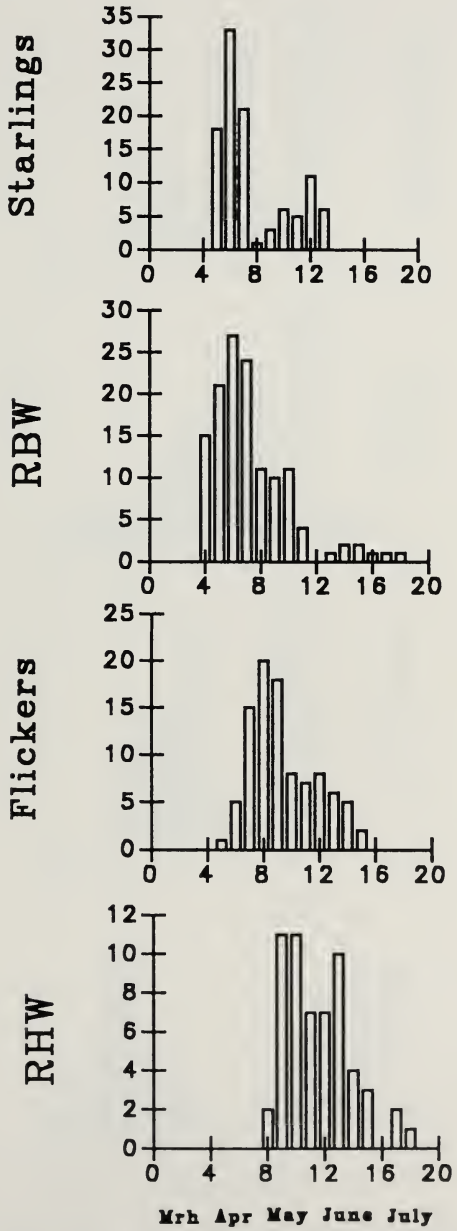

FIG. 1. Number of starling and woodpecker pairs involved in nest construction during 1990–1992 (N = 45 starling pairs, 40 RBW pairs, 42 flicker pairs and 23 RHW pairs; weeks on x axes).

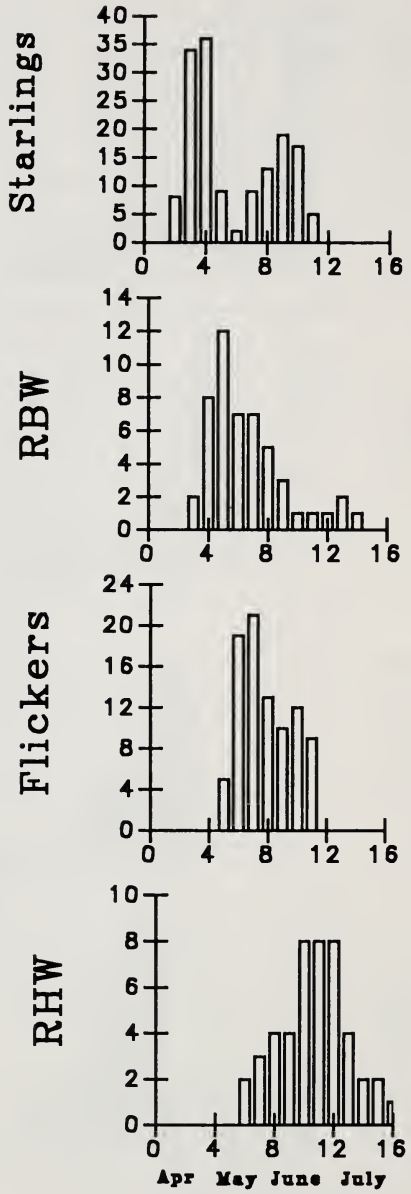

FIG. 2. Number of starling and woodpecker pairs incubating eggs during 1990–1992.

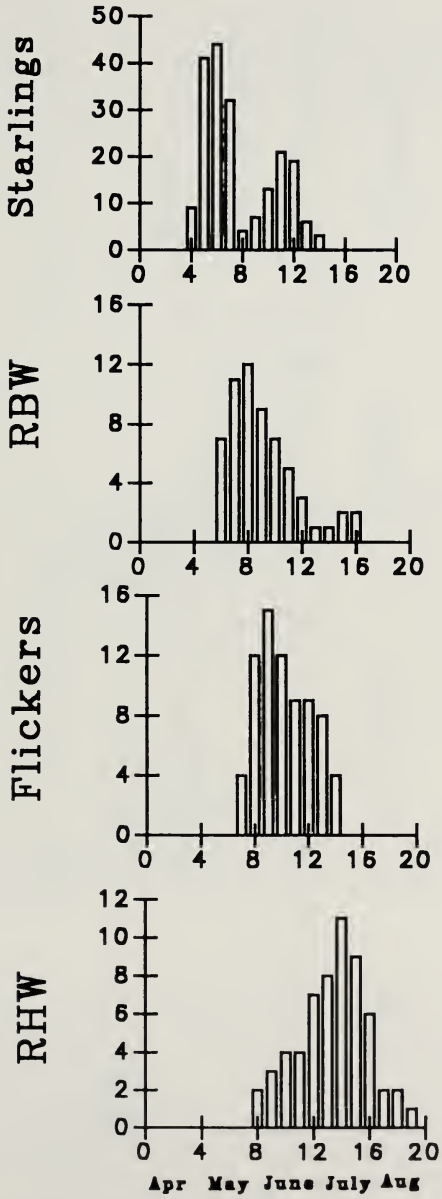

FIG. 3. Number of starling and woodpecker pairs with nestlings during 1990–1992.

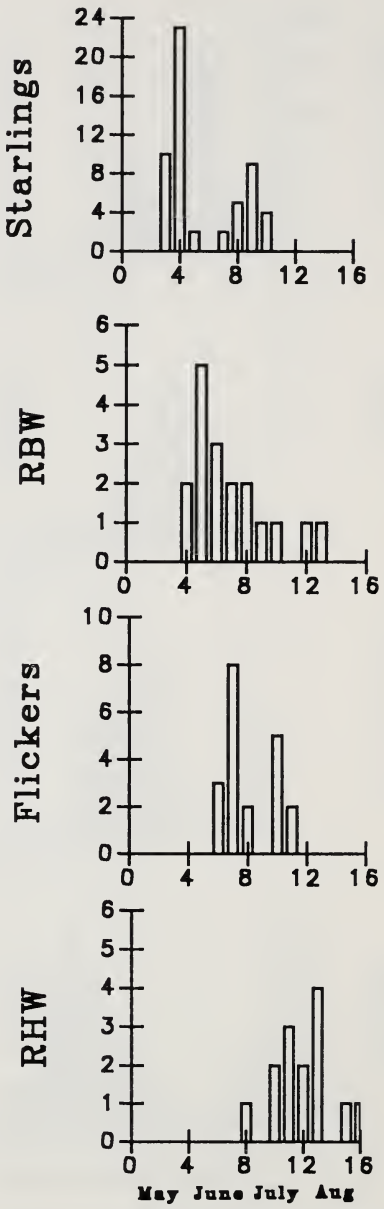

FIG. 4. Number of staring and woodpecker pairs with fledglings during 1990–1992.

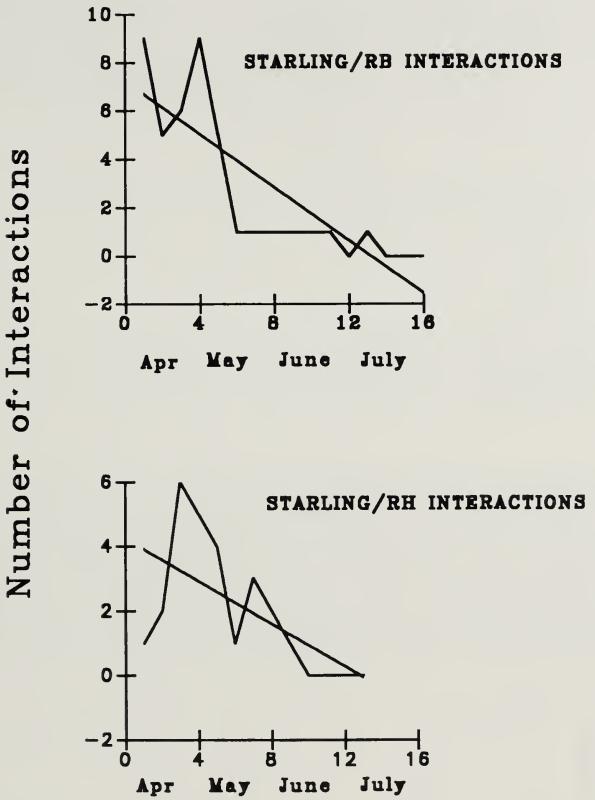

FIG. 5. The relationship between time and the number of starling/Red-bellied Woodpecker interactions per week (top; $Y = 7.23 - 0.549X$; $r^2 = 0.68$) and starling/Red-headed Woodpecker interactions per week (bottom; $Y = 4.23 - 0.33X$; $r^2 = 0.41$) during 1990–1992.

negatively associated with the progression of time ($F = 5.28$, df = 1,12; $P < 0.05$; $r^2 = 0.37$), and only one cavity was usurped after 31 May. In addition, RBWs lost three cavities to flickers, two to southern flying squirrels (*Glaucomys volans*), and one to House Sparrows (*Passer domesticus*), relinquishing a total of 50% of their nest cavities to other species.

Seven of 51 flicker nest cavities (14%) were usurped by starlings from April through June (Fig. 6). In addition, flickers lost two cavities to RHWs and two to black rat snakes (*Elaphe obsoleta*), thus surrendering 22% of their cavities. RHWs lost four of 27 (15%) of their cavities to starlings, mostly during May (Fig. 6) and two additional cavities to House Sparrows. Because the number of starling/flicker and starling/RHW cavity usurpations was small, I did not perform regression analyses.

TABLE 1

SUMMARY OF COMPETITIVE INTERACTIONS BETWEEN STARLINGS AND WOODPECKERS AT OR NEAR NEST CAVITIES DURING 1990–1992

Aggressor species ("winner")	Intimidated species ("loser")				Totals
	Starling	RBW	NF	RHW	
Starling	—	32	16	12	60 (65%)
RBW[a]	9	—	5	0	14 (23%)*
NF	10	8	—	6	24 (41%)*
RHW	13	8	14	—	35 (66%)

[a] RBW = Red-bellied Woodpecker; NF = Northern Flicker; RHW = Red-headed Woodpecker. Numbers in the totals column denoted with an asterisk are significantly different from undenoted numbers ($P < 0.01$) (contingency table chi-square tests).

Of 32 woodpecker cavities usurped by starlings, at least 22 (69%) were eventually abandoned by the starlings before egg laying. At least 11 of 18 RBW pairs (61%) that lost cavities to starlings eventually excavated a new cavity in the same ½ circular ha or reclaimed their original cavity, but only four of these pairs (36%), to my knowledge, eventually fledged young. At least three of seven flicker pairs (43%) and three of four RHW

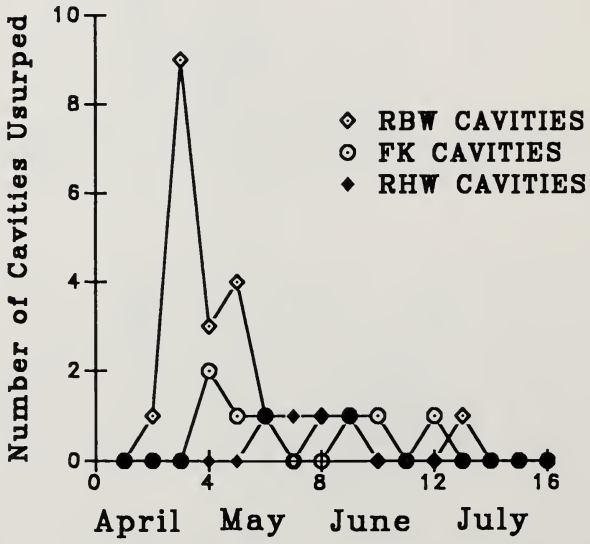

FIG. 6. Timing of cavity usurpations by European Starlings and Red-bellied Woodpeckers (RBW), Northern Flickers (NF), and Red-headed Woodpeckers (RHW) during 1990–1992 (weeks on x axis).

pairs (75%) also excavated a new nest cavity in the same ½ circular ha or reclaimed their old cavity, and of these, one flicker pair and two RHW pairs eventually fledged offspring.

DISCUSSION

These data suggest that interference competition (Levine 1976, Maurer 1984) between starlings and three woodpecker species does occur in east-central Ohio and is perhaps common. RBWs were particularly vulnerable to starling harassment, in part because they initiated nesting at the same time as starlings in early April; in addition, they were significantly less aggressive than starlings and other woodpeckers when defending their nest cavities. Ingold (1989a, b) documented a similar trend in Mississippi in which RBWs lost 52% of all their cavities to starlings and were significantly less aggressive than RHWs and starlings in competitive encounters.

The nesting phenology of Northern Flickers overlapped with starlings to a lesser extent, and they were also less vulnerable to starling harassment than were RBWs. By the time many flicker pairs completed cavity excavation in late April and early May, many starling pairs had already secured nest cavities and were incubating eggs. Those flickers that did encounter persistent starling harassment proved vulnerable despite their larger size. Although flickers were slightly more aggressive than RBWs, they were significantly less aggressive than starlings and RHWs when defending their nest cavities. In May 1993, I observed an attack by an adult starling on an adult flicker near a nest tree on my study site in which the starling clung to the back of the flicker while on the ground and pecked it repeatedly. Eventually, when the starling detected my presence, the flicker escaped and flew from the area. This observation, and my data in general, contrasts with those of Kerpez and Smith (1990) who found that flickers did not encounter starling competition in areas of sympatry in Arizona.

By initiating nesting in early May, RHWs were able to avoid most starling competition, since most starlings were well into their first nest effort by this time. However, not all starlings were able to find suitable nest cavities in April, and RHWs did loose 15% of their cavities to starlings, mostly in May. RHWs were as aggressive as starlings during competitive encounters at nest cavities and were often successful in driving them away. Ingold (1989a, b) found that RHWs in Mississippi lost only 7% of their nest cavities to starlings and were significantly more aggressive than starlings in head-to-head encounters.

Although nesting starlings were abundant in town and on the Muskingum campus, few woodpecker pairs (4 of 105; 4%) were found in

these areas. Although excavated cavities on campus and in town appeared to be in short supply, natural knot cavities were plentiful. In fact 28 of 32 (88%) town-nesting starlings used natural cavities in six trees in which two or more starling pairs nested concomitantly within a few m of each other in knot holes. Conversely, 17 of 23 nesting starling pairs (74%) in the country used old or freshly excavated woodpecker cavities, suggesting that such cavities are more readily available and perhaps preferred over natural cavities. Although Ingold (1989b) commonly found nesting woodpeckers in town and on campus in Mississippi it is likely that the abundance of town starlings in this study discouraged many woodpeckers from undertaking nesting efforts in town.

There are advantages in maintaining differences in nesting phenologies of RBWs, flickers, and RHWs in areas where they are sympatric. However, the persistent selection pressure of starling competition could alter the timing of nesting of these species. Indeed, one consequence of interspecific competition is that it may result in a shift in the niche of one or more of the competing species (Diamond 1978, Grant 1986). Despite differences in nest-site preferences among these woodpeckers (Selander and Giller 1959; Mayr and Short 1970; Jackson 1976; Short 1982; Kilham 1977, 1983), they occasionally competed for nest sites, mostly in late April and May. RBWs are often able to avoid most nest-site competition with other woodpeckers (cf Ingold 1989a) by initiating nesting in late March and early April. On the other hand, they must compete with early-nesting starlings for nest sites. Those RBWs and other woodpeckers that are able to avoid starling competition should be at a selective advantage. However, if they delay the onset of nest initiation to avoid starlings (i.e., a niche shift), they risk increasing the period of competitive overlap with other woodpeckers which could also adversely affect their reproductive efforts.

Although my data suggest that nest-site competition is occurring, particularly among starlings and RBWs, I have only indirect evidence to suggest that one or more of the woodpecker species are suffering reductions in fecundity as a result of starling interference. Even though at least 59% of the woodpecker pairs that lost their cavities to starlings eventually returned to the same area to excavate a new cavity or reclaim an old cavity, only about 40% of these pairs eventually fledged young. Those woodpecker pairs that did not return may have also fledged young. To my knowledge, only a single woodpecker pair attempted a second brood after a successful first one. Thus, a delay in nesting caused by starlings may not be detrimental to woodpeckers if they can still fledge some young later in the season. On the other hand, such a delay may not only promote interspecific competition between woodpeckers, but it could also expose

them to food shortages and warmer temperatures that might adversely affect their reproductive success. Van Balen and Cave (1970) and Mertens (1977) found that Great Tit (*Parus major*) nestlings that hatched after the end of May were at a greater risk of incurring hyperthermia, thus reducing their chances of survival. Perhaps an even greater problem associated with such a delay might be the degree of maturity and experience that fledglings have acquired by the time winter begins. Woodpeckers produced by later nestings may be at an experience disadvantage relative to woodpeckers produced earlier in the nesting season. This could be of particular importance at more northern latitudes where winter begins much sooner than in the south. In any case, adaptive strategies resulting from starling/woodpecker competition for nest cavities in Ohio are still emerging. Competing woodpeckers (particularly RBWs) may shift their nesting efforts to later in the season to avoid starlings, or they could nest in more densely forested areas where starlings are scarce. It is also possible that selection may favor more aggressive woodpeckers over time, because such pairs would have a higher probability of producing young that would survive to breed.

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SNAG CONDITION AND WOODPECKER FORAGING ECOLOGY IN A BOTTOMLAND HARDWOOD FOREST

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Abstract.—We studied woodpecker foraging behavior, snag quality, and surrounding habitat in a bottomland hardwood forest in the Stephen F. Austin Experimental Forest from December 1984 through November 1986. The amount and location of woodpecker foraging excavations indicated that woodpeckers excavated mainly at the well-decayed tops and bases of snags. Woodpeckers preferred to forage on oaks (*Quercus* spp.) (snags and live trees) whereas blue beech (*Carpinus caroliniana*) and red maple (*Acer rubrum*) were used less than expected. Snags used for foraging excavations were generally 3–10 m in height, mainly located in older stands, and lacked bark at excavated foraging sites. In the bottomland habitat, Downy Woodpeckers (*Picoides pubescens*) foraged on smaller diameter substrates and used more tree species than other woodpecker species. Pileated Woodpeckers (*Dryocopus pileatus*) foraged either near the ground or in the upper zones of trees. Red-bellied Woodpeckers (*Melanerpes carolinus*) used a restricted range of tree diameters and locations in trees. Red-headed Woodpeckers (*M. erythrocephalus*) used the greatest diversity of foraging methods and foraged on the largest range of tree diameters. *Received 27 April 1993, accepted 12 Aug. 1993.*

Many woodpecker species depend on snags (standing dead trees) for foraging sites (Kisiel 1972, Conner 1980, Mannan et al. 1980, Brawn et al. 1982, Raphael and White 1984, Morrison and With 1987). Until recently (Rosenberg et al. 1988), little attention has been focused on the characteristics of snags associated with high quality foraging. Because characteristics of snags may vary regionally, it is important to examine snag use relative to condition in a variety of forest types. In addition, the value of snags as nesting and roosting sites for woodpeckers and other cavity nesters is well known (Conner 1978, Evans and Conner 1979, Thomas et al. 1979, Raphael and White 1984).

Bottomland hardwood forests are dwindling and typically have relatively abundant woodpecker populations. More than 63% of the original southeastern bottomland hardwood forests have been lost, and the current rate of loss per decade in eastern Texas is about 14% (USFWS 1984). Knowledge of the sizes, species, bark condition, and decay conditions of

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snags and trees that are used by woodpeckers is important for the provision of such habitat in this critical habitat type. Determination of forest structure that is conducive to snag formation could aid management of such habitat.

We examined woodpecker foraging behavior, snag size and condition, and surface area of foraging excavations on snags to evaluate snag quality and woodpecker foraging ecology in bottomland hardwood forests. Forest stand structure around snags was evaluated to determine what environmental conditions are associated with snags that have high use by foraging woodpeckers.

STUDY AREA AND METHODS

The study area (28.7 ha) was centrally located in a bottomland hardwood forest on the floodplain of the Angelina River in the Stephen F. Austin Experimental Forest (31°29′N, 94°47′W) in southern Nacogdoches County, Texas. Of 1038 ha of forested bottomland habitat in the experimental forest, approximately 650 ha are in the flood plain. The study area contained 66.7 snags/ha (10.2% of vertical stems) and 585 live hardwoods/ha (89.8%) (Jones 1987). The last timber harvest occurred on the experimental forest in 1920 when some high value trees were logged selectively. The dominant trees by percentage of live hardwoods were sweetgum (*Liquidambar styraciflua*), oak species [including water oak (*Quercus nigra*), overcup oak (*Q. lyrata*), Nuttall's oak (*Q. nuttallii*), willow oak (*Q. phellos*), swamp chestnut oak (*Q. michauxii*)], blue beech (*Carpinus caroliniana*), and black gum (*Nyssa sylvatica*). The average diameter at breast height (DBH) of all trees (including snags) with a DBH of 10 cm or more was 23.4 cm; the average height of these trees was 33.2 m (Jones 1987). A mid-story layer of blue beech, eastern hop-hornbeam (*Ostrya virginiana*), water elm (*Planera aquatica*), and hollies (*Ilex* spp.) was present. The soils of the bottomland are of the Manatachie series (U.S. Soil Conservation Service 1980) and are poorly drained and highly acidic. The water table is near the surface, and water depths of up to 1.5 m can persist for up to two months.

We collected data on snags, live trees, surrounding habitat, and woodpecker foraging behavior from December 1984 through September 1986.

Vegetation and study tree measurements.—Forty-three snags, seven live trees with dead portions, and 10 live trees were selected randomly (using a spinning pointer at systematically selected fixed points) from their respective populations during January 1985 to provide a variety of tree species and substrate conditions ranging from well-decayed to minimal or no decay. Selected trees (study trees) were greater than 12 cm DBH and far enough apart (>25 m) so that plots did not overlap. Snag species (based on bark characteristics), height (clinometer), and DBH (diameter tape) were measured while trees were standing. We measured tree density, relative density, dominance, relative dominance, frequency, relative frequency, and importance value (see Curtis and McIntosh 1951) within a 0.04 ha ($\frac{1}{25}$ ha) circular plot (11.3 m radius) around each study tree (Conner 1980). We calculated average DBH and basal area of all live hardwoods and snags (≥12 cm DBH) from diameter measurements (Table 1). We divided trees into three DBH size classes (class one = 10–18 cm; class two = 19–38 cm; and class three = >38 cm) to reflect sapling, pole, and sawtimber-sized trees.

In June 1986, we felled 52 of the 60 study trees (8 were deemed too dangerous to fell), measured, and divided them into four equal-length bole zones: lower, lower middle, upper middle, and upper. We measured the percentage of residual bark attached to each snag within each height zone (e.g., percentage of residual bark on the lower zone) on the exposed

TABLE 1

CHARACTERISTICS OF ENVIRONMENTAL VARIABLES MEASURED IN 0.04 HA PLOTS CENTERED ON 60 STUDY TREES IN A BOTTOMLAND HARDWOOD FOREST IN EASTERN TEXAS

Variable	Mean	SD	Range
Dominant vegetation height (m)	33.2	8.4	18.9–50.3
Basal area of live hardwoods (m^2 per 0.04 ha)	1.4	0.7	0.1–3.0
Basal area of snags (m^2 per 0.04 ha)	0.3	0.3	0.0–1.4
Live hardwoods per 0.04 ha plot	23.4	9.8	8.0–47.0
Snags per 0.04 ha plot	2.7	1.6	1.0–7.0
Logs per 0.04 ha plot	4.7	3.1	0.0–14.0
Average diameter at breast height (cm)	24.1	4.3	16.5–37.7
Class one: number of trees (10–18 cm) per 0.04 ha plot	14.4	7.1	4.0–38.0
Class two: number of trees (19–38 cm) 0.04 ha plot	7.4	4.2	0.0–23.0
Class three: number of trees (>38 cm) per 0.04 ha plot	4.3	1.9	0.0–8.0
Number of tree species per 0.04 ha plot	7.1	2.0	3.0–11.0
Distance to water (m) (sloughs or creeks)	33.4	26.0	0.0–100.0

portion of the bole in each zone and extrapolated for the entire circumference. Because some bark was dislodged during felling, darkened, moist areas of the bole were measured as if they still were covered by bark. An average of the percentages of residual bark for each zone yielded the percentage for the entire study tree.

Pilodyn® measurements of sapwood hardness.—We measured tree hardness within each of the four height zones. A two-joule Proceq pilodyn® was used to measure wood hardness (Sprague et al. 1983). A pilodyn® fires a precision spring-loaded steel pin into the sapwood with a constant force measuring penetration depth (mm). If present, we removed bark at measurement sites to allow direct access to the sapwood. Three measurements per height zone were taken and averaged. We made measurements within 3 cm of woodpecker foraging sites when excavation holes were present. If woodpecker foraging sites were not present, we made measurements in the middle portion of each height zone at three equidistant positions around the circumference of the bole. Penetration depth is inversely related to wood hardness.

Specific gravity determinations of study tree sapwood.—As a relative indicator of extent of decay, we extracted a wood sample (approx. 1 × 3 cm) from each of the four height zones of each felled study tree to determine the sapwood's specific gravity. Decay by basidiomycetes in trees oxidizes lignin and cellulose, softens the wood, and replaces structural wood with air (Cartwright and Findlay 1958, Overholts 1977). Thus, for a given tree species, lower specific gravity values indicate more fungal decay. We extracted wood samples from sites within or adjacent to foraging sites to measure more precisely specific gravity of wood (decay extent) where woodpeckers had foraged. If woodpecker foraging sites were not present, we extracted wood samples in the middle portion of each height zone at three equidistant positions around the circumference of the bole. Specific gravity was measured and calculated

using the two formulas described by Smith (1954) and values averaged because results varied by as much as 0.08 g.

Measurement of woodpecker foraging sign and arthropods on study trees.—We measured the surface area of woodpecker foraging sign (pecking, scaling, and excavation, later converted to percentage of the bole with woodpecker foraging sign) on the boles of felled study trees by height zone. Five ellipses representing common excavation sizes observed on snags (1, 7, 50, 72, and 97 cm^2) were drawn on cardboard in the field and measured with a Licor® LI-3000 electronic portable area meter in the lab. We measured/estimated the surface area of all visible foraging sites by comparing the nearest ellipse size to the foraged area for each of the four bole height zones. If the foraged area lay between sizes or was larger than the largest ellipse, an estimation was made. Because approximately 25% of the tree's surface was on the ground, and not visible, the final summation for each height zone was made by dividing the measured amount by three and multiplying the quotient by four. The total surface area of each height zone was calculated using height and diameter measurements in order to determine the percentage of the bole's surface excavated by woodpeckers. We did not include excavations that clearly appeared to be cavity starts in our measurements of foraging sign. Use of only signs of pecking, scaling, and excavation obviously misses indications of woodpecker foraging that involved peer-and-poke foraging and other superficial gleaning techniques.

We assumed that foraging sign indicated the presence of arthropod prey because nearly all excavation sites penetrated beetle, ant, or termite galleries (live arthropods were regularly observed) that were hidden within the bole, thus, indicating the quality of study tree height zones as foraging sites. Variable time periods elapsed between when woodpeckers foraged on study trees and our measurement of foraging sign. However, the relative differences of foraging sign among height zones on individual trees should accurately reflect woodpecker use of the different zones. We did not determine the species of woodpecker that actually made the excavations on study trees.

To test the assumption that foraging sign indicated the presence of arthropod prey, we removed two blocks of wood (approximately 20 × 20 × 15 cm) from the upper and lower height zones on each study tree. We removed these wood samples from portions of the snags where woodpecker foraging sign was absent. Arthropods that emerged and those obtained during subsequent dissection of the blocks of wood were identified to order and counted (Borror and White 1970). Arthropod samples were oven dried at 85°C to constant weight.

Behavioral observations on foraging woodpeckers.—We observed foraging behavior on initial contact with Downy (*Picoides pubescens*) (N = 189), Pileated (*Dryocopus pileatus*) (N = 100), Red-bellied (*Melanerpes carolinus*) (N = 111), and Red-headed (*M. erythrocephalus*) (N = 250) woodpeckers throughout the year from December 1984 to September 1986. Although Hairy Woodpeckers (*Picoides villosus*), Yellow-bellied Sapsuckers (*Sphyrapicus varius*), and Northern Flickers (*Colaptes auratus*) were present, we collected insufficient data on these species for inclusion. We timed the duration of foraging behaviors, as well as the behavior at the initial time of contact with a woodpecker with a stop watch, and recorded the information on a cassette recorder. Visibility often was difficult, especially during the summer months when a dense canopy cover reduced light and a thick mid-story and sometimes dense understory obscured observations of foraging woodpeckers. Typically, durations of behavioral observations were very short due to foliage obscuring woodpeckers and bird movements. This was a particular problem with Pileated Woodpeckers because of their wariness.

We divided foraging methods into six behaviors (revised from Conner 1981) and noted foraging location within the tree. Peer-and-poke foraging was limited to surface gleaning.

Scaling involved active removal of bark in search of food items. Excavating was differentiated from pecking when the cambial layer was penetrated. Hawking and foraging on logs were also noted. We measured the locations of foraging woodpeckers on trees (trunk, branch, twig) and conditions (live, dead part of live, snag) of the foraging substrates. Branches were lateral stems larger than 2 cm in diameter, whereas twigs were stems <2 cm in diameter.

Analyses.—We used Chi-square analyses and Bonferroni's test (Miller 1981, Byers et al. 1984) to evaluate woodpecker foraging preference among tree species. A wide range of substrate conditions (snags to live trees) was selected to permit examination of correlative relationships, or discriminant analysis if low and high use sites tended to be bimodal. A frequency histogram using the amount of woodpecker foraging sign revealed a bimodal distribution with a midpoint equally dividing the sample of study trees. Snags (dead trees and live trees with dead portions) with foraging sign on >6% of the total surface area were grouped as "high use" foraging sites (N = 25), whereas those with ≤6% were considered "low use" foraging sites (N = 25). We used Mann-Whitney *U*-tests and *t*-tests to compare the surrounding habitats and characteristics of high and low use snags. We tested for heterogeneity of variances between groups during *t*-tests and selected appropriate significance probabilities based on variance equality (SAS 1988).

We also used two-group discriminant analysis to compare high and low use snags. Box's *M* test indicated that group covariance matrices were homogeneous ($P = 0.35$), a necessary assumption for discriminant analysis. Prior probabilities of classification for the discriminant analysis were set equivalent to sample sizes.

We used one-way analysis of variance (ANOVA, $P < 0.05$) to examine woodpecker foraging behaviors, and Chi-square and Bonferroni's test (Byers et al. 1984) to examine the foraging preferences among the woodpeckers for particular tree species. We used correlation analysis to examine relationships among woodpecker foraging sign, arthropod biomass, snag hardness, and specific gravity.

RESULTS

Vegetative characteristics of the study area.—Characteristics of study trees and surrounding habitat varied extensively, providing a range of sites for woodpecker foraging (Tables 1 and 2). Sweetgum and oaks were the most frequent species in the plots (Table 3). We were unable to identify the species of 15% of the snags. Only black gum snags occurred at a higher frequency than its live hardwood counterpart, indicating either a higher snag formation rate or a slower decay rate than other tree species.

A total of 1404 live hardwoods (35.4 m^2/ha basal area), 1 loblolly pine (*Pinus taeda*), and 160 snags (6.7 m^2/ha) comprising 20 tree species were present within the 60 study plots (Table 1). Snags comprised 10.2% of all trees in the study site. Based on importance values, the dominant overstory species (excluding snags) were sweetgum, black gum, water oak, and over-cup oak. The upper canopy layer was dense and uniform except where fallen trees, sloughs, and creek channels existed. Blue beech, red maple (*Acer rubrum*), and species with small DBH's such as deciduous holly (*Ilex decidua*) comprised the midstory. Live trees between 12 and 18 cm diameter (811 trees) comprised 58% of the study

TABLE 2

CHARACTERISTICS OF THE 60 STUDY TREES IN A BOTTOMLAND HARDWOOD FOREST ON THE STEPHEN F. AUSTIN EXPERIMENTAL FOREST

Variable	Mean	SD	Range
Study tree height (m)	9.3	5.4	2.4–25.9
Diameter at breast height (cm)	37.2	17.9	12.0–83.0
Wood hardness lower (mm)	29.3	12.4	7.0–45.0
Wood hardness lower middle (mm)	25.0	13.4	6.0–45.0
Wood hardness upper middle (mm)	28.2	13.4	6.0–45.0
Wood hardness upper (mm)	32.3	12.8	3.0–45.0
Wood hardness of total tree (mm)	28.7	11.6	3.0–45.0
Percentage of bark lower zone	61.1	39.3	0.0–100.0
Percentage of bark lower middle zone	66.0	35.2	0.0–100.0
Percentage of bark upper middle zone	63.1	37.6	0.0–100.0
Percentage of bark upper zone	34.6	37.4	0.0–100.0
Percentage of bark total tree	56.4	29.1	0.0–100.0
Specific gravity lower zone	0.3	0.1	0.1–0.6
Specific gravity lower middle zone	0.3	0.1	0.1–0.7
Specific gravity upper middle zone	0.3	0.1	0.1–0.7
Specific gravity upper zone	0.3	0.1	0.1–0.6
Specific gravity total tree	0.3	0.1	0.1–0.7

area, trees 19 to 38 cm (382 trees) 27%, and trees >38 cm (212 trees) 15%. Most of the sweetgum trees were in the smallest size class, while black gums were mainly >38 cm DBH. No blue beech was recorded larger than 18 cm.

TABLE 3

FREQUENCIES OF LIVE HARDWOODS AND SNAGS, AND PERCENTAGE OF TREE SURFACE AREA WITH WOODPECKER FORAGING SIGN IN A BOTTOMLAND HARDWOOD FOREST

Tree species	Frequency of live hardwoods (%) N = 1404	Frequency of snags (%) N = 160	Amount of woodpecker foraging sign (%)
Sweetgum	31.6	25.5	29.8
Oak species	29.8	24.9	42.4[a]
Blue beech	12.0	8.1	0.7[b]
Black gum	10.7	16.2	22.9
Red maple	8.6	3.1	1.6[b]
Unidentified	0	15.5	
Others	7.3	6.8	2.7[b]

[a] Bonferroni's test, $P < 0.05$, foraging intensity significantly greater than expected.
[b] Bonferroni's test, $P < 0.05$, foraging intensity significantly less than expected.

TABLE 4

COMPARISON OF SNAGS (N = 50) WITH EXTENSIVE FORAGING SIGN (>6%) WITH SNAGS USED LESS FREQUENTLY (≤6%) USING A TWO-TAILED *t*-TEST

Snag variable	Foraging sign >6%	Foraging sign ≤6%	*t*	*P*
Snag height (m)	7.6 (25)	10.8 (25)	2.05	0.046
Snag DBH (cm)	37.9 (25)	36.5 (25)	0.28	0.785
Snag hardness lower (mm)	34.8 (23)	23.5 (22)	3.37	0.002
Snag hardness lower middle (mm)	30.0 (23)	19.8 (22)	2.72	0.010
Snag hardness upper middle (mm)	34.1 (23)	22.1 (22)	3.33	0.002
Snag hardness upper (mm)	37.5 (23)	26.8 (22)	3.06	0.004
Percent bark lower (%)	46.6 (23)	76.3 (22)	2.70	0.010
Percentage bark lower middle (%)	53.5 (23)	81.0 (22)	2.82	0.007
Percentage bark upper middle (%)	55.2 (23)	71.4 (22)	1.46	0.151
Percentage bark upper (%)	26.1 (23)	43.4 (22)	1.58	0.122
Specific gravity lower	0.32 (23)	0.31 (22)	0.17	0.864
Specific gravity lower middle	0.31 (23)	0.35 (22)	1.33	0.191
Specific gravity upper middle	0.26 (23)	0.31 (22)	1.55	0.130
Specific gravity upper	0.27 (23)	0.31 (22)	0.90	0.374

Discriminant analysis ($P < 0.032$, overall classification success was 72%) using environmental variables was calculated to compare high use snags (N = 25) with low use snags (N = 25). Snags exhibiting high use by foraging woodpeckers were located in habitat that had a higher basal area of live hardwoods ($r = 0.76$, $P < 0.01$, correlation of original variable with the discriminant function), larger average diameter trees ($r = 0.66$, $P < 0.01$), and more trees >38 cm ($r = 0.51$, $P < 0.01$) than habitat with low use snags.

Woodpecker foraging sign on study trees and arthropod biomass.— Woodpeckers foraged on certain tree species more than others ($\chi^2 = 152.3$, $P < 0.001$); oaks were most preferred (Table 3). Woodpecker foraging sign on sweetgum approximated its frequency of occurrence, whereas blue beech and red maples were used less than expected. The pilodyn® typically penetrated live trees only 9–15 mm. Higher pilodyn® values indicate greater decay because of deeper penetration of the striker pin. Lower values of specific gravity indicate greater decay. Trees with signs of high foraging use consistently yielded average pilodyn® readings of over 30 mm, indicating a softer, more decayed condition (Table 4). Specific gravity measurements of all tree species combined were highly correlated ($r = -0.768$, $P < 0.001$) with pilodyn® measures of hardness (Table 5). Short and soft snags had the greatest amount of foraging sign (Table 4). Snags with extensive foraging sign were also in more advanced

TABLE 5
PEARSON CORRELATIONS OF PERCENTAGE OF SNAG SURFACE AREA WITH WOODPECKER FORAGING SIGN AND SNAG QUALITY VARIABLES

Snag quality variables	Woodpecker foraging sign	Snag height	Snag DBH	Snag hardness	Percent bark
Snag height	−0.358[a]				
Snag DBH	−0.140	0.459[a]			
Snag hardness	0.473[a]	0.005	0.432[a]		
Percent bark	−0.191	0.212	0.316	−0.109	
Specific gravity	−0.376[a]	−0.081	−0.452[a]	−0.768[a]	−0.142

[a] $P < 0.01$.

stages of decay (Mann-Whitney, $U = 145.5$, $P < 0.001$; see snag hardness, Table 4).

Woodpecker foraging sign was more prevalent in the highest ($\bar{x} = 3.3\% \pm 3.6$ (SD), range = 0 to 14.5) and lowest ($\bar{x} = 3.5\% \pm 4.2$, range = 0 to 57.9) height zones of the snags. Evidence of woodpecker foraging was less abundant in the upper middle ($\bar{x} = 1.8\% \pm 2.6$, range = 0 to 13.4) and lower middle ($\bar{x} = 2.1\% \pm 3.0$, range = 0–13.4) zones. The location of woodpecker foraging sign (above), percentage of residual bark, and snag hardness at the four standardized height zones (Table 4) collectively indicate that woodpeckers foraged most often on the well-decayed, softer portions of snags (Fig. 1). The percentage of residual bark on snags was inversely related to the amount of woodpecker foraging sign; and residual bark was least at the top and base of snags where evidence of woodpecker foraging sign was greatest. It is difficult to say whether the absence of bark promotes or is caused by woodpecker foraging.

Arthropod biomass of the entire study tree was significantly correlated with the amount of woodpecker foraging sign ($r = 0.76$, $P < 0.0001$) and specific gravity of snags ($r = -0.49$, $P < 0.001$) but not with pilodyn® measurements of snag hardness ($r = 0.24$, $P < 0.15$). Although not significant, snags that exhibited high use foraging sign had a dry weight arthropod biomass ($\bar{x} = 0.28$ g $\pm$ 0.87, $t = 1.23$, $P = 0.23$) more than five times greater than low use snags ($\bar{x} = 0.05$ g $\pm$ 0.07). Arthropods collected from study trees included 21 orders: Isoptera (36%), Coleoptera (27%), Hymenoptera (22%), Arachnida (4%), Collembola (3%), Orthoptera (2%), and all others (6%). Most arthropods were collected from the bottom portions of study trees (338 of 532 arthropods).

Observations of foraging woodpeckers.—Although there was considerable foraging sign on the 60 study trees, woodpeckers were only rarely

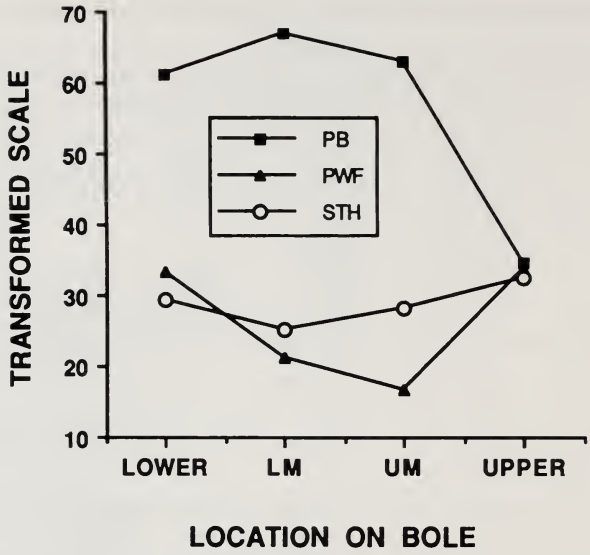

FIG. 1. Percentage of tree surface foraged on by woodpeckers (PWF), percentage of intact bark (PB), and study tree hardness (STH) at the four height zones on snags (lower, lower middle [LM], upper middle [UM], and upper) in the bottomland forest on the Stephen F. Austin Experimental Forest in eastern Texas. Higher values for snag hardness indicate more extensive decay (greater pilodyn® penetration means increasing softness).

observed using them. Live trees (live trees and live trees with dead branches) were selected most often as foraging sites by Downy (N = 189, 45%), Pileated (N = 100, 68%), and Red-bellied (N = 111, 62%) woodpeckers in the bottomland hardwood forest habitat, whereas Red-headed Woodpeckers used live trees the least (N = 250, 48%). Downy Woodpeckers used snags 23% of the time, Pileated's 31%, Red-bellied's 30%, and Red-headed's 48%. When snags and dead portions of live trees are combined, Downy (55%) and Red-headed woodpeckers (80%) foraged mainly on dead wood, whereas Pileated (32%) and Red-bellied (38%) woodpeckers foraged primarily on live wood.

Downy Woodpeckers foraged more on twigs (53%) than Pileated (0%), Red-bellied (5%), and Red-headed (2%) woodpeckers. Pileated (70%) and Red-bellied (75%) woodpeckers mainly selected branches as foraging sites, whereas Red-headed (48%) and Downy (25%) woodpeckers foraged on branches to a lesser extent. Red-headed Woodpeckers (50%) foraged on trunks more often than Downy (23%), Pileated (30%), and Red-bellied (20%) woodpeckers.

Woodpecker species foraged at significantly different heights when us-

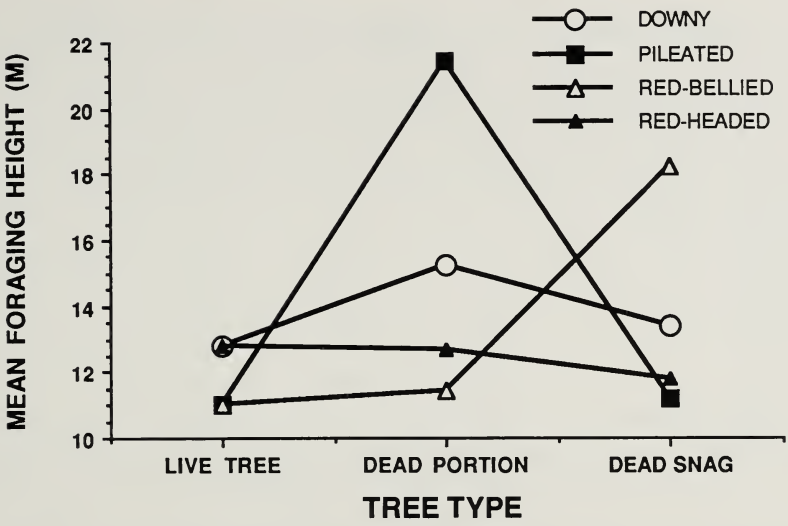

FIG. 2. Mean foraging height in meters of Downy, Pileated, Red-bellied, and Red-headed woodpeckers on live trees, dead portions of live trees, and snags in a bottomland hardwood forest on the Stephen F. Austin Experimental Forest in eastern Texas.

ing different tree conditions (live trees, dead parts of live trees, or snags) (Two-way ANOVA, $P < 0.006$). Downy Woodpeckers used higher sites when foraging on dead parts of live trees and snags than on live trees (Fig. 2). Pileated Woodpeckers foraged at about the same height when foraging on live trees and snags, but used higher sites when on dead parts of live trees. Red-bellied Woodpeckers foraged highest when using snags. Red-headed Woodpeckers varied foraging heights the least when using different tree conditions (Fig. 2).

Downy Woodpeckers foraged upon the largest variety of woody species (Table 6). Pileated Woodpeckers were observed foraging on only four tree species. Bonferroni's test indicated that all woodpecker species preferred to forage on oaks at a higher frequency than their availability and tended to avoid red maples and blue beeches as foraging sites ($P < 0.05$). As also observed by Conner (1979, 1980), Downy Woodpeckers usually stayed at about the same height when moving from tree to tree, typically foraging for a short time period before flying to the next tree. Downy Woodpeckers foraged on the greatest number of tree species as observed by Jackson (1970) and Conner (1980, 1981). Pileated Woodpeckers in our study and others foraged upon the fewest tree species and, in general, appear to be more restrictive in their use of tree species (Bull and Meslow 1977, McClelland 1979, Conner 1981, Kilham 1983).

TABLE 6

PERCENTAGES OF TREE SPECIES FORAGED UPON BY FOUR SPECIES OF WOODPECKERS IN A BOTTOMLAND HARDWOOD FOREST ON THE STEPHEN F. AUSTIN EXPERIMENTAL FOREST

Tree species	Downy	Pileated	Red-bellied	Red-headed
Blue beech	4.5			
Flowering dogwood				4.7
Sweetgum	36.4	33.3	9.1	16.3
Black gum	9.1	13.3	18.2	23.3
Water elm	2.3			
Pine species	4.5	20.0	9.1	4.7
Poison ivy	2.3			
Oak species	34.1	33.4	36.4	37.2
Slippery elm	2.3			
Unidentified snags	4.5		27.3	14.0

Downy Woodpeckers primarily pecked while foraging on twigs of live trees (Fig. 3). Pileated and Red-bellied woodpeckers foraged using the peer-and-poke method more than either pecking or excavating. Red-headed Woodpeckers frequently pecked at substrates while foraging but

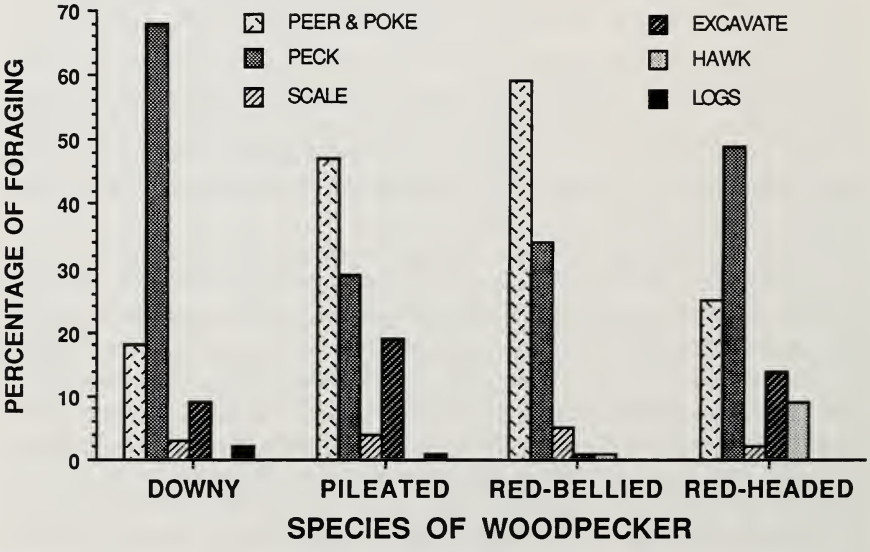

FIG. 3. Frequencies of foraging methods used by Downy (DW), Pileated (PW) Red-bellied (RBW), and Red-headed (RHW) woodpeckers in a bottomland hardwood forest on the Stephen F. Austin Experimental Forest in eastern Texas.

also hawked insects, fed on vegetable matter, and/or foraged on the ground.

DISCUSSION

Both tops and bases of snags were preferred foraging sites for woodpeckers. Ground moisture and flooding at the base of snags and rain soaking the tops may have increased micro-climate humidity and facilitated softening by fungal decay and use by arthropods. Extent of decay appears to be an important indicator of overall snag quality in southern bottomland hardwoods because extent of decay and woodpecker foraging sign were highly correlated with arthropod biomass.

Woodpecker excavations were more frequent on the softer portions of snags, on shorter snags, and on snags in advanced stages of decay in general. This suggests possible relationships among snag age, decay, and height. However, no correlation between snag height and degree of decay was detected (Table 5). Shorter snags are probably older snags (Cline et al. 1980) and would have had a longer time period for decay to occur and woodpeckers to forage on them. However, this would likely be a relatively short period of time in the hot, humid climate of southern bottomland forests because such conditions hasten decay (Cartwright and Findlay 1958, Overholts 1977). Rosenberg et al. (1988) found that woodpeckers had an apparent preference to forage in tall snags in Virginia and that this preference appeared to be the result of a positive diameter–height relationship.

Specific gravity and snag hardness as measured by the pilodyn® (all tree species combined) were highly correlated indicating that pilodyn® measurements are an excellent relative estimate of decay. Previous studies have indicated the similarity of pilodyn® and specific gravity as measures of wood density in forest products studies of undecayed wood samples (Cown 1978, Sprague et al. 1983). We prefer use of the pilodyn® because of its ease of use compared to specific gravity measurements, and it may more closely measure the resistance felt by excavating woodpeckers. However, specific gravity was highly correlated with arthropod biomass whereas pilodyn® measurements were not.

Bark texture (rugosity) within and among tree species may affect arthropod abundance and resulting use of snags by woodpeckers (Jackson 1979). Variability in bark roughness was associated with seasonal differences in foraging behavior of Downy Woodpeckers (Travis 1977). The bark of oaks, black gum, and sweetgum is more deeply fissured than bark of blue beech and red maples. Woodpeckers foraging in the bottomlands on both live and dead trees may have avoided tree species with smooth bark because of a paucity of arthropods.

Oaks were important to foraging woodpeckers both as snags and live trees. Woodpeckers preferentially foraged on oaks and tended to avoid blue beech and red maple. Oaks were among the largest diameter snags in the bottomland whereas blue beech and red maple had the smallest diameters of the most abundant five species of snags (Jones 1987). Although this suggests that tree diameter may have influenced snag selection, results of univariate analyses did not support the importance of large diameter snags as woodpecker foraging sites in southern bottomland hardwood forests. Tree diameter has been shown to be a significant criterion for foraging site selection by woodpeckers in other studies. Mannan et al. (1980), Brawn et al. (1982), and Rosenberg et al. (1988) all found that woodpeckers preferred large diameter snags.

Foraging preferences for particular tree species have been reported in various studies (Willson 1970; Travis 1977; Conner 1980, 1981; Kilham 1983). As in our study, oaks are preferred foraging sites by woodpeckers across a wide range of timber types and geographical regions (Willson 1970, Short 1971, Reller 1972, Williams and Batzli 1979, Conner 1980, Kilham 1983). Oaks in Mississippi had a high (59%) infestation rate of oak borers (Solomon 1969), suggesting the importance of oak borers as a food resource.

Seven species of woodpeckers are indigenous to the bottomland hardwood forest of eastern Texas: Downy, Hairy, Pileated, Red-headed, and Red-bellied woodpeckers, Northern Flicker, and Yellow-bellied Sapsucker. All are permanent residents except the Yellow-bellied Sapsucker which is a winter resident and the Northern Flicker which tends to be migratory. Of these the Downy, Red-bellied, Pileated, and Red-headed woodpeckers, and Yellow-bellied Sapsuckers (winter) are common in the bottomlands whereas Hairy Woodpeckers occur infrequently. Northern Flickers, Yellow-bellied Sapsuckers, and Red-headed Woodpeckers do not normally excavate in trees for food as do other woodpecker species (Reller 1972, Conner 1979, Tate 1973). Because woodpecker species foraging on snags (study trees) were not identified, relationships between snag quality and diameter at breast height that have been observed by others (Mannan et al. 1980, Brawn et al. 1982, Rosenberg et al. 1988) may have been obscured. Also, some of the smaller excavations may have resulted from Tufted Titmouse (*Parus bicolor*) and Carolina Chickadee (*P. carolinensis*) foraging (Conner 1978).

Pileated Woodpeckers in our study foraged more on live trees than generally reported elsewhere (Bull and Meslow 1977, McClelland 1979, Conner 1980). This may reflect a more abundant arthropod community on the surface of live trees in the relatively warm southern forests than the more northerly forests examined in the previous studies. Pileated

Woodpeckers, however, seemed particularly wary of observers, and this may have influenced detection of snag use.

Analyses indicated that snags with extensive foraging sign were found in stands where basal area of live hardwoods, tree diameter, dominant vegetation height, and number of trees greater than 38 cm DBH were high. Collectively, these variables suggest that woodpeckers selected snags that were located in older growth areas, or that preferred snags were found predominantly in older growth areas. Management favoring old-growth bottomland hardwood forests and protection of large diameter oak snags may benefit woodpeckers that forage by excavation. Pileated Woodpeckers excavated more than other woodpecker species in our study area and would benefit the most from provision of large, well decayed oak snags.

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PATTERNS OF MORTALITY IN NESTS OF RED-COCKADED WOODPECKERS IN THE SANDHILLS OF SOUTHCENTRAL NORTH CAROLINA

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ABSTRACT.—Mean clutch size of Red-cockaded Woodpeckers (*Picoides borealis*) in the sandhills of southcentral North Carolina was 3.3 eggs, mean brood size was 2.3 nestlings, and the mean number of young fledged per successful nest was 1.9 fledglings. Many groups (9–25%, depending on year) did not nest at all. We estimated the total mortality rate of young for the entire nesting period to be 43% (range 31.8–49.5%). Total mortality was significantly higher for second nesting attempts than for first attempts. Also, nests initiated early in the nesting season had significantly lower mortality rates than those begun later in the season. Rates of whole brood loss were typical for temperate cavity-excavators, but partial brood loss was high. Whole brood loss usually occurred during incubation or soon after hatching. Of first nesting attempts, 21.6% failed to produce fledglings. Renesting was attempted by 13–61% of groups which failed, depending on year, and 0–50% of these attempts failed. Whole brood mortality rates increased significantly during 1980–1985. Whole brood loss appeared to be caused more often by other cavity-using species than by predators. Partial brood losses resulted from the loss of nestlings and the production of eggs that failed to hatch (at least 7.1%), including runt eggs (1.1% of all eggs). Losses of nestlings typically occurred between hatching and when young were 6 days of age, suggesting brood reduction. Mortality rates were significantly higher at this stage than for the preceding (incubation) and following (late nestling and early fledging) periods. Few nestlings were lost between banding (usually at age 5–10 days) and fledging checks (usually at ages 27–50 days, 1–14 days after fledging). Partial brood loss due to parasites appeared negligible, despite continuous use of individual cavities for as long as the duration of the study. *Received 15 July 1992, accepted 15 Sept. 1993.*

Understanding the population dynamics of endangered animals is critical to efforts to save these species. To describe population dynamics one must document demographic parameters (survival and fecundity) that characterize the natural population. Understanding population dynamics requires quantifying variation in reproduction and survival and identifying the environmental factors responsible for this variation. Based on knowledge of how environmental factors affect population dynamics, prescriptions for management to improve survival and reproduction can then be developed. In the present paper we analyze the population dynamics of the endangered Red-cockaded Woodpecker (*Picoides borealis*) based on data from a population in the sandhills of southcentral North Carolina. Data were collected over a six-year period from as many as 200 nests/

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yr. We present nest mortality rates and patterns of variation and discuss our results with respect to other studies of Red-cockaded Woodpecker (RCW) reproduction, population dynamics, and management.

METHODS

The study area (110,000 ha) is described in detail by Carter et al. (1983) and Walters et al. (1988). It contains three major areas of concentration of birds with intervening areas of lower bird density. The dominant vegetation is longleaf pine (*Pinus palustris*) with a predominantly scrub oak (*Quercus* spp.) understory. It contains about 550 adult birds which is about half the local RCW population (Walters et al. 1988). Nearly all (95%) of the birds were uniquely marked with color bands.

Data were collected from all known nests from 1980 through 1985. A typical Red-cockaded Woodpecker territory contains several cavity trees (Ligon 1970, 1971; Lay et al. 1971), referred to as a "cluster". At the beginning of each breeding season, each cluster was checked for evidence of active RCW use employing Jackson's (1977) criteria. Each active cluster was checked from early April until late July or until the group succeeded in producing at least one fledgling. In 1982 and 1983, clusters were checked for nesting activity approximately every 14 days; in all other years they were checked every nine days. All trees with active cavities were checked by tapping and scraping on the tree. When an adult appeared in the entrance, flushed from a cavity, or was observed in the vicinity, the tree was climbed and the cavity contents were recorded. If no nest was found in a cluster during the second cycle of nest visits, all active cavity trees were climbed and checked for evidence of nesting. In clusters where nesting attempts failed or where no nest was found, all active trees were climbed regularly, especially when adults were seen or heard nearby.

When a nest was found, the number of eggs, nestlings, and/or fledglings and their age and sex (if known) were recorded. The nest was then checked in each subsequent cycle of nest visits. Nestlings were aged using criteria in Ligon (1971). Each nestling, at age 4 days or older, was uniquely color banded, aged, and weighed.

For each nest in which young were banded, date of fledging (at age 26 days) was estimated, and fledging checks were conducted as soon after this date as possible. Nests were not revisited between banding and the fledging check. During the fledging check, the group was followed until its size was determined and all fledglings present were identified and sexed from crown patches. Male fledglings have a patch of red in their crown, whereas females do not (Ligon 1970). Any group missing a previously-banded nestling was followed at least twice to confirm that the bird had not fledged. Most fledging checks exceeded one hour; when birds were missing, total time spent following them frequently exceeded three hours. More than 99% of fledglings were detected using this procedure (Walters et al. 1988).

The young were aged when they were banded or during some other nest check during the nestling stage. For each nest, we calculated ages of eggs, nestlings and fledglings at the time of other checks of that nest by back- and fore-dating from the banding age or other known age. We adjusted some ages ± two days if the calculated clutch initiation day or hatch day did not match previous observations. For example, if only eggs and no nestlings were seen on a day calculated as nestling age 1 day, we set this date as age −1 day and adjusted all other ages for checks of that nest accordingly. The length of incubation is reported to be 10 or 11 days (Ligon 1970, Lennartz and Harlow 1979). For ease of calculations, we designated the day of hatch as age 0 days and the incubation period as −11 to −1 days. All eggs in a clutch are usually laid by day −11.

We considered clutches complete, and thus the clutch size known, if eggs in a nest were counted during the eleven days before hatch (−11 to −1 days) or if the count was consistent

on two checks during the egg stage. Since aging was done only for nestlings, age of nests lost during the egg stage could not be determined. Therefore, we did not include data from these nests in analyses of partial brood loss.

We considered eggs inviable if present in nests with nestlings at least three days old. Some eggs were noted as being smaller than normal, usually in comparison to the others present in the clutch. Eggs were not measured and records of small eggs are likely to be inconsistent among the observers. However, when these eggs were noted, it is probable that the size difference between the eggs was extreme. These eggs do not necessarily meet the criteria used in identifying runt eggs in studies of other species (see Koenig 1980a).

We described the patterns of mortality for eggs, nestlings, and fledglings following Mayfield's (1961, 1975) methods. The Mayfield method was appropriate during the period up to and including the date of banding, since nest check cycles were 14 da or fewer in all years (Johnson 1979). However, after banding, the nestlings usually were not visited again until after they fledged, a period that was typically 20 to 30 da.

We computed mortality rates and variances (Johnson 1979) for the periods preceding and following hatching for all nests, nests with known clutch sizes, and all successful nests. We compared mortality rates using Z-tests (Johnson 1979, Bart and Robson 1982). To look for seasonal trends, each nesting season was divided into two-week intervals starting with the first nest of the year. We also compared first nesting attempts to renests.

We examined whole and partial brood losses separately. Those nests that lost part of a brood initially and the remainder of the brood at a later time, were used in both sets of analyses. We calculated mortality rates for partial loss of a brood (PBL) using Mayfield's method (1961, 1975) for only those nests with known clutch sizes. Mortality rates for nest failure or whole brood loss (WBL) were also calculated by Mayfield's method. For each analysis, we divided the data into three age periods: incubation, 0–6 days, and 7+ days, to determine the timing of mortality.

RESULTS

Groups that contained at least one adult of each sex were considered potentially able to produce a nest. Increases in numbers of groups from one year to the next reflected increases in the area included in the study or the pairing of previously solitary male territory holders rather than formation of new territories (Table 1). The total number of nest attempts recorded and the number of fledglings produced were both highest in 1984 (Table 1). A highly variable proportion (9–25%; mean 17.4%) of potentially breeding groups failed to nest each year (Table 1).

Incubation commenced in mid-April, occurring as early as 13 April in 1985 and as late as 22 April in 1980. Date of last nest initiation was more variable among years and ranged from 23 May in 1985 to 3 July in 1983. Mean clutch size was consistently greater than three eggs (Table 2). Although data on renesting attempts were insufficient for detailed analysis, there was no obvious clutch size difference between first and second attempts. Mean clutch size was not correlated to the mean number of nestlings (Kendall Test for Independence, $\tau = 0.20$, $P = 0.72$) or fledglings ($\tau = 0.07$, $P = 1.00$) (Table 2). However, means for nestlings and fledglings were highly correlated ($\tau = 0.87$, $P = 0.016$).

TABLE 1

NUMBER OF GROUPS MONITORED[a], NESTS, FLEDGLINGS, AND GROUPS WITH NO RECORDED NEST

Year	Groups	Nests	Fledglings	Groups not nesting
1980	109	94	171	20
1981	183	160	294	28
1982	179	139	216	44
1983	185	157	223	38
1984	193	203	336	17
1985	203	176	243	36

[a] Increases in number of groups usually reflects the addition of groups not previously included in the sample.

Inviable eggs were frequently produced. In most years, 5–7% of all eggs seen were inviable by our definition (see above) (Table 3). In all years combined, 23 eggs (1.1% of all eggs seen) were reported to be runts. Of these, two were known to hatch, and 16 (69.6%) were inviable or were lost in a failed clutch. One female produced eight of these runt eggs in three attempts over two years.

Most nests were found before hatching occurred (Table 4). Many nests were found later in 1981 than in other years because the study area was expanded during the breeding season. Ninety-five percent of all nests observed were found by age 11.5 days. Median banding age for all years combined was 8 days (s^2 = 15.9), and 95% were banded by day 16 (Table 4). During 1981–1983, age of banding was higher than in the three other years because of longer nest check intervals. Half of all fledglings were seen within a week after fledging (by day 33), and 95% were seen by age 50 days.

TABLE 2

MEAN CLUTCH SIZE, MEAN NUMBER OF NESTLINGS PER NEST AND MEAN NUMBER OF FLEDGLINGS PER SUCCESSFUL NEST FOR NESTS OF KNOWN CLUTCH SIZE

Year	Mean clutch size	Mean number of nestlings	Mean number of fledglings
1980	3.18	2.27	1.98
1981	3.18	2.36	2.04
1982	3.20	2.26	1.86
1983	3.24	2.11	1.66
1984	3.47	2.53	2.07
1985	3.21	2.22	1.65
All years	3.27	2.31	1.88

TABLE 3
PERCENT OF INVIABLE EGGS

Year	Number of eggs seen	Percent inviable
1980	232	12.1
1981	262	6.5
1982	244	6.6
1983	370	8.6
1984	598	5.6
1985	469	5.5
All years	2175	7.1

Mortality Patterns

For all years combined, daily mortality rate for first attempts increased with the period of the season in which the nest was initiated (Kendall $\tau = 0.8$, $P = 0.05$; Fig. 1). This pattern was not found in renesting attempts, but for both first and second attempts the variance of the mortality rate increased significantly over the season ($\tau = 0.8$, $P = 0.05$). The percent of nests from which all eggs hatched and all young were observed as fledglings decreased steadily through the season ($\chi^2_3 = 15.3$, $P < 0.005$; Fig. 2). In 1984, the only year with sufficient data for analysis, females of age 1 initiated first attempts significantly later in the season than females older than age 1 ($\chi^2_3 = 22.6$, $P < 0.005$).

First nesting attempts had significantly lower mortality rates than second attempts in three years (Fig. 3; *Z*-test: $P = 0.19$, 0.0084, 0.25, 0.028, <0.0001, 0.15, for 1980–1985 respectively). The variances of these rates for second attempts differed by an order of magnitude from that of first

TABLE 4
MEDIAN AGES OF YOUNG WHEN NESTS WERE FIRST DISCOVERED, WHEN NESTLINGS WERE BANDED AND WHEN A FLEDGING CHECK WAS FIRST MADE

Year	Median age at discovery	Median age at banding	Median age at fledging check
1980	−7	7	28
1981	0	9	31.5
1982	−1	11	36.5
1983	−4	10	37
1984	−7	7	32
1985	−7	7	34
All years	−5	8	33

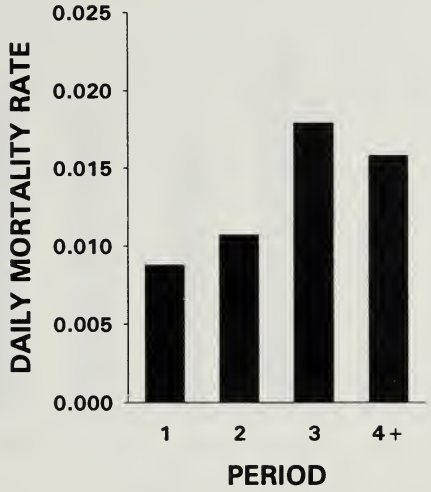

FIG. 1. Daily mortality rates for first nesting attempts initiated in two-week periods during the nesting season (all years combined). Rates increase significantly throughout the season.

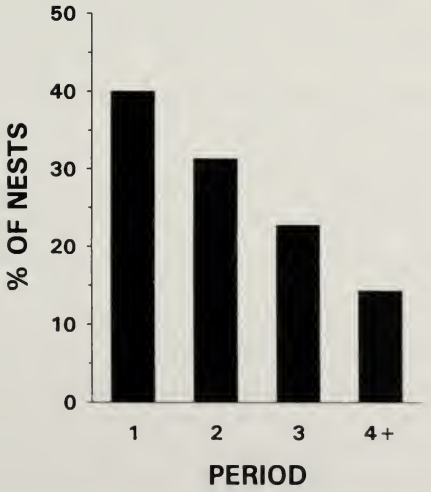

FIG. 2. Percent of nests in which all eggs layed produced fledglings in nests initiated during two-week periods in the nesting season (all years combined).

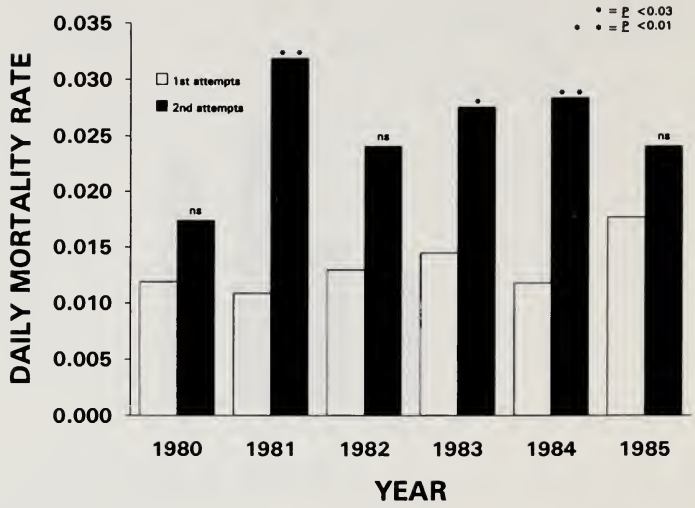

FIG. 3. Daily mortality rates for first and second nesting attempts. Rates are significantly different in three years (Z-test).

attempts. Almost 34% of first attempts had no brood loss at all compared to 9.8% for second attempts. Differences between attempts were confounded with seasonal effects, since second attempts occurred later in the nesting season. Also, renests were attempted by groups that had already failed at their first attempt and thus may have been prone to failure, for example because they had poor territories or were comprised of young individuals.

For all years combined, 22.1% of the nests discovered experienced whole brood losses. Of first nesting attempts, 21.6% resulted in WBL (Table 5). The frequency of renesting was variable among years: 13.8–61.4% of failed first attempts were followed by renesting. One group nested three times in 1984, a phenomenon that had not been observed previously in RCWs. In this case, the first two nests both resulted in early (egg stage) WBL.

The daily rate of WBL, calculated by Mayfield's exposure method, was 0.0061 (s^2 = 0.00003); the rate for the entire nesting period was 0.2725. Rate of WBL increased significantly from 1980 to 1985 (Mann Trend Test, P = 0.008).

Most WBL occurred before nestlings were seen in the nest. For all nests, the nest mortality rate for the period following the first observation of nestlings was 0.08, and the observed frequency of nest loss for this same time period was 8%. This suggests that use of the Mayfield method

TABLE 5

PERCENT OF WHOLE BROOD LOSS (WBL) FOR FIRST NESTING ATTEMPTS, PERCENT OF FAILED FIRST ATTEMPTS FOLLOWED BY RENESTING AND PERCENT WHOLE BROOD LOSS FOR RENESTING ATTEMPTS

Year	Number of first attempts	Percent WBL of first attempts	Percent renesting	Percent WBL of renests
1980	89	14.6	38.5	0.0
1981	154	11.7	33.3	50.0
1982	135	21.5	13.8	50.0
1983	150	26.0	25.6	30.0
1984	177	24.9	61.4	44.4
1985	167	26.9	22.2	20.0
All yrs	872	21.6	33.0	35.5

for calculating this mortality rate was appropriate. The mortality rate for nests before nestlings were seen was 0.207, and the frequency of nest loss for such nests was 14.0%. We thus estimate that 20.7% of all (known and unknown) nests were lost before nestlings were seen and that 6.7% of all nests failed before their discovery. In the six years of the study, 929 nests were observed. We therefore estimate that in the six years 67 nests failed prior to detection. Thus, some nests counted as first attempts were actually second attempts, and some groups recorded as failing to nest actually nested but failed quickly. Still, at least 10 groups per year (116 total, 11% of all groups) did not nest.

We believe that very few nests were missed during the nestling period. In support of this assumption, one group in each of five years (0.5% of all known nests) was reported to have fledglings when no nest was previously reported.

Although causes of WBL were usually unknown, field notes associated with nest failures frequently mentioned other occupants in the nest cavity. Twenty-six WBLs (12.7% of all known WBL) occurred in cavities that later were reported to have another species nesting or roosting in them. Chief among these other species were southern flying squirrels (*Glaucomys volans*), Red-bellied Woodpeckers (*Melanerpes carolinus*), and Red-headed Woodpeckers (*M. erythrocephalus*). In addition, 15 groups that did not have a known nest (10.5% of non-nesting pairs) had cavities usurped by other species. Another known cause of WBL was fires that charred the tree and cavity (three known nest losses, one possible).

PBL mortality rates were significantly higher for the early nestling (0–6 days) age interval in each year (Fig. 4; Z-test, $P = 0.0084$, 0.0014, <0.0001, <0.0001, <0.0001, <0.0001, for 1980–1985 respectively). The

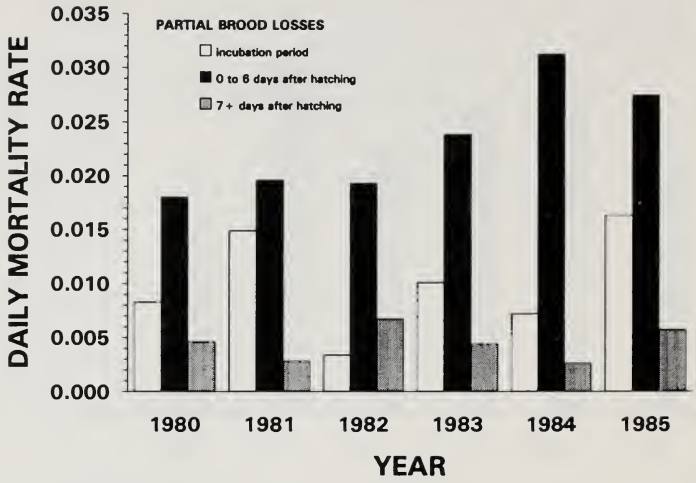

FIG. 4. Daily mortality rates for different stages of nesting in different years. Rates are significantly higher in the early nesting period than in the incubation and late nestling periods in each year (Z-test, $P = 0.01$).

PBL mortality rate from the start of incubation to fledging was 0.2719 for all years combined. Annual variations in WBL and PBL mortality rates were not correlated (Kendall Test for Independence, $\tau = 0.552$, $P = 0.126$). Although WBL mortality rates increased from 1980 to 1985, PBL rates did not (Mann Trend Test, $P = 0.136$). However, combining both types of mortality (PBL and WBL) the mortality rate per individual increased significantly from 1980 to 1985 (Mann Trend Test, $P = 0.028$).

DISCUSSION

The estimated number of nests missed (6.7%) is small considering the length of the nest-check intervals. The two years with longer (14-day) nest-check intervals did not have a higher frequency of missed nests than the years with nine-day cycles. This suggests that, for the purpose of recording nesting attempts, nest check cycles as long as 14 days are acceptable. However, for calculating mortality rates, nine-day cycles are more appropriate. By using this shorter cycle, rates can be calculated for specific stages of the nesting period, especially the incubation and early nestling stages. With the longer cycle the mortality rates for the stages within the nesting period are more likely to be biased.

The mean clutch size of 3.27 in our study agrees with values reported in other studies of this species (Ligon 1970, 1971; Baker 1971; Lennartz and Harlow 1979). The effects of age and timing of clutch initiation on

reproductive success observed are typical of avian species (Lack 1954, 1968; Perrins 1970; Clutton-Brock 1988). Age appears to have a particularly pronounced effect on reproductive success in Red-cockaded Woodpeckers, especially among males (Walters 1990). Groups in which the breeding male is only one year old account for many of the observed cases in which groups failed to nest (Walters 1990).

WBL and PBL are roughly equally important in brood mortality in RCWs, and their timing is similar as well. Both act primarily in the first half of the nesting period. Minimal losses occur after the young have reached age six days. The rate of WBL is comparable to other cavity-excavators in the temperate zone (Martin and Li 1992), but PBL is unusually high (total loss 27% versus 17% in other species, Nilsson 1986).

The loss of part of a brood early in the nestling stage, as occurs in Red-cockaded Woodpeckers, suggests brood reduction. This is thought to be an adaptation that enables the parents to match the number of young fledged to the food resources available (Lack 1954, 1968). It involves the early (soon after hatching) loss of the younger and smaller of asynchronously hatched nestlings, usually by starvation, when food is insufficient (O'Connor 1978). Significant partial brood loss is consistently observed in this species (Ligon 1970, 1971; Lay et al. 1971; Harlow 1983; Lennartz et al. 1987). In addition, incubation begins before the clutch is complete, hatching is asynchronous and nestling size discrepancies are typical (Ligon 1970, 1971; Walters et al., unpubl. data). That the early loss of RCW nestlings is due to starvation has yet to be verified, but all indirect evidence indicates that brood reduction is characteristic of the RCW. We detected no fluctuations in the extent of brood reduction indicative of adjustments to resource conditions.

Not all PBL can be attributed to brood reduction, however. Some was due to eggs failing to hatch. Since all eggs were not seen, and since inviable eggs could have been removed from the cavity before being noted by observers, 7.1% is undoubtably an underestimate of the percentage of eggs that failed to hatch.

Few studies of nesting in birds quantify hatching failure, usually noting only that some eggs are known not to hatch (e.g., Howe 1976, Murphy 1983). The percentages reported here do not, however, appear to be extreme. Custer and Pitelka (1977) reported 17.1% hatching failure in studies of Lapland Longspurs (*Calcarius lapponicus*) and Zach (1982) found hatching success to be 78–95% for Tree Swallows (*Tachycineta bicolor*).

Interestingly, there was no indication that parasites, a leading cause of PBL in many cavity-nesters (Nilsson 1986), were a significant mortality factor in RCWs. Ectoparasites were observed and recorded while handling the nestlings during banding. Although the same cavities are often used

for nesting for several years, only rarely did we observe significant nest infestations.

In addition to inviable eggs, some runt eggs were noted in RCW nests, as reported elsewhere (Ramey and Jackson 1979). Runt eggs may contribute to those eggs that fail to hatch. Among North American woodpeckers that are not cooperative breeders, the occurrence of runt eggs is uniformly low (range: 0–0.797%) (Koenig 1980b). For RCWs, Koenig (1980b) reported 1.33% of 75 eggs in museum collections were runts, a value similar to the (minimum) value reported here. Koenig (1980b) suggests that cooperative breeding may contribute to the overproduction of runt eggs in Acorn Woodpeckers (*Melanerpes formicivorous*). Our data provide additional evidence of a link between cooperative breeding and the production of runt eggs.

The presence of other occupants in former nest cavities indicates that loss of cavities to other species may be responsible for much WBL. Other species are known to usurp RCW cavities (Carter et al. 1989). In addition, destruction of RCW nests has been noted. Other bird species remove RCW eggs, and southern flying squirrels crush and possibly eat the eggs (pers. obs.). Because dead trees are easily destroyed by the frequent fires associated with this habitat and only RCWs construct cavities in live trees, Godfrey (1977) suggested that both secondary and other primary cavity nesters in pine savannas "rely" on RCWs to construct cavities. This could lead to unusually high levels of nest losses in RCWs compared to other cavity-excavators.

That most WBL occurred early in the nesting cycle suggests that nest desertion is a major cause of WBL (Ricklefs 1969). Frequent nest desertion might be related to the complex social system of this species. Lack of correlation between PBL and WBL suggests that starvation of young is not a major component of WBL. Loss of broods to predators such as snakes appears to be exceptionally infrequent, even for a cavity excavating species (Walters 1990). This presumably reflects the effectiveness of the pine resin barrier produced by the birds around their cavities (Rudolph et al. 1990).

Variation in reproductive output between years was a function of WBL and the proportion of groups that did not nest. Others also have noted that some potentially breeding groups of RCWs fail to nest (Hopkins and Lynn 1971, Wood 1983). Such events may be related to occupation of cavities by other species. However, variation in failure to nest was not correlated with variation in WBL, as it should be if usurpation of cavities during the nesting season was a factor in both. Instead, variation in failure to nest was correlated with variation in renesting. Years in which the highest proportion of groups nested also had the highest renesting rate

when broods failed (Kendall Test $P = 0.068$, Tables 1, 5). This suggests annual variation in reproductive effort. Perhaps individuals whose chances of success are low forego breeding when conditions are poor. One-year-old males have the lowest success rate of any age-sex class when they attempt nesting and also are most likely to fail to nest (Walters 1990).

The patterns observed suggest few opportunities to increase reproduction through management. One possibility is that WBL, and perhaps failure to nest, could be reduced by reducing usurpation of RCW cavities by other species. Some studies have suggested that frequency of cavity usurpation of RCW cavities is positively related to development of hardwood understory (Jackson 1978), others that it is related to availability of snags in the vicinity of the cluster (Harlow and Lennartz 1983). Everhart (1986) found no evidence for either relationship in our study area. Clearly, additional research is needed to determine whether reducing use of RCW cavities by other species can improve RCW reproduction. We are currently testing this hypothesis experimentally using metal plates (restrictors; Carter et al. 1989) that restrict access of some other species to RCW cavities at the cavity entrance.

ACKNOWLEDGMENTS

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PREDATOR-PREY INTERACTIONS BETWEEN EAGLES AND CACKLING CANADA AND ROSS' GEESE DURING WINTER IN CALIFORNIA

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Abstract.—Cackling Geese (*Branta canadensis minima*) were preyed on heavily in northeastern California by Golden Eagles (*Aquila chrysaetos*) and less commonly by Bald Eagles (*Haliaeetus leucocephalus*) in 1985–1990. Eagle predation on Cackling Geese was minimal in other wintering locations in California. In the Klamath Basin, eagles killed Cackling Geese most frequently soon (<10 days) after the geese arrived in the fall. Eagles killed fewer Cackling Geese in the Klamath Basin when Cackling Geese were less common than Ross' Geese (*Chen rossii*) and Lesser Snow Geese (*C. caerulescens caerulescens*). We also examined spatial and temporal (daily, seasonal, and annual) variation in eagle predation on geese at a smaller scale in Big Valley, California. Most eagle-caused flushes of geese occurred during mid-day when the geese were using traditional day-roost sites. Roosting on water with most other Cackling and Ross' Geese in Big Valley reduced the frequency of eagle attacks relative to other sites. In Big Valley, the larger Great Basin Canada Goose (*Branta canadensis moffitti*) was attacked by Golden Eagles only once during 88 observation days, while the smaller Cackling and Ross' geese were attacked by Golden Eagles a total of 27 times. Moreover, Cackling Geese in Big Valley were attacked and killed at least twice as often as Ross' Geese because Cackling Geese often grazed in pasture where Golden Eagle attacks were more frequent. When feeding on pasture, geese did not increase time spent vigilant or flock size compared to habitats with less eagle predation. The antipredator behavior of Cackling Geese includes maintaining high levels of vigilance, occurring in large, dense flocks, and roosting on water during nonfeeding periods. When attacked by eagles, Cackling Geese used socially-coordinated and speed-based escape tactics. *Received 2 June 1993, accepted 15 Sept. 1993.*

An individual bird may join a flock to reduce the chance of being attacked or of being caught when attacked (see Bertram 1978). Birds in flocks may be safer than solitary individuals for at least three reasons. Individuals in a group may detect predators better or earlier than smaller groups or solitary individuals (Pulliam 1973, Siegfried and Underhill 1975, Kenward 1978, Lazarus 1979). A predator which attacks a group of prey may become confused and catch fewer prey (Neill and Cullen 1974, Milinski 1979, Landeau and Terborgh 1986). Finally, an individual in a group may reduce its chance of being caught simply because of a dilution-effect (Foster and Treherne 1981).

Flocking creates a tradeoff between avoiding predators and feeding efficiently (Powell 1974, Caraco 1979a, b, Caraco et al. 1980, Pulliam

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and Caraco 1984, Poysa 1987). Individuals in larger groups generally enjoy greater protection from predators, but as groups become larger the antipredator benefits may diminish and costs associated with, for example, foraging and social dominance may increase (reviewed by Curio 1976, Pulliam and Caraco 1984, Black 1988, Elgar 1989).

We investigated the predator/prey relationship between eagles and Cackling Geese (*Branta canadensis minima*), Great Basin Canada (*B. canadensis moffitti*), and Ross' (*Chen rossii*) Geese on wintering areas in California. Golden (*Aquila chrysaetos*), and particularly Bald Eagles (*Haliaeetus leucocephalus*), congregate in many of the same areas as waterfowl during winter in northeastern California, making interactions between eagles and geese frequent and observable. We measured variation in the frequency of eagle predation on Cackling Geese at two spatial scales (geographic and local) and three temporal scales (annual, seasonal, and daily). We evaluated some causal mechanisms for this variation in predation risk. We then explored whether Cackling Geese modify their flock size or time spent vigilant in response to variation in the risk of eagle predation.

Although direct predation on adults has minor impacts on population dynamics of geese (reviewed by Owen 1980), predators may strongly influence avian systems through effects on behavior and distribution of birds rather than through direct mortality (reviewed by Lima and Dill 1990, Lima 1993). Cackling Geese are among the smallest geese in North America, averaging about 1.5 kg in winter (Raveling 1978). Their small body size may lead to increased predation risk and account for some of their unique social organization (Johnson and Raveling 1988, Owen and Black 1990, McWilliams and Raveling, in press). Where Cackling and Ross' Geese form mixed species flocks in northeastern California, they often occur sympatrically with the larger Great Basin Canada Goose. In this paper, we compare the frequency of eagle predation on sympatric Great Basin, Cackling, and Ross' geese in Big Valley, California. Such interspecific comparisons reveal how differences in body size of geese influences risk of eagle predation which then may influence goose social behavior.

METHODS

An intensive study of the numbers, distribution, and annual survival of neck-banded Cackling Geese was conducted during winter, 1982–1983 through 1987–1988 (Raveling et al. 1992). Before fall 1985, observations of eagle activity were not consistently recorded. Three observers in 1985–1986 and two observers in 1986–1987 observed Cackling Geese from dawn until dusk almost daily between mid-October through late-April. In 1987–1988, we spent fewer days observing geese, and we concentrated our effort primarily in Klamath Basin, Sacramento Valley, and San Joaquin Valley (Fig. 1).

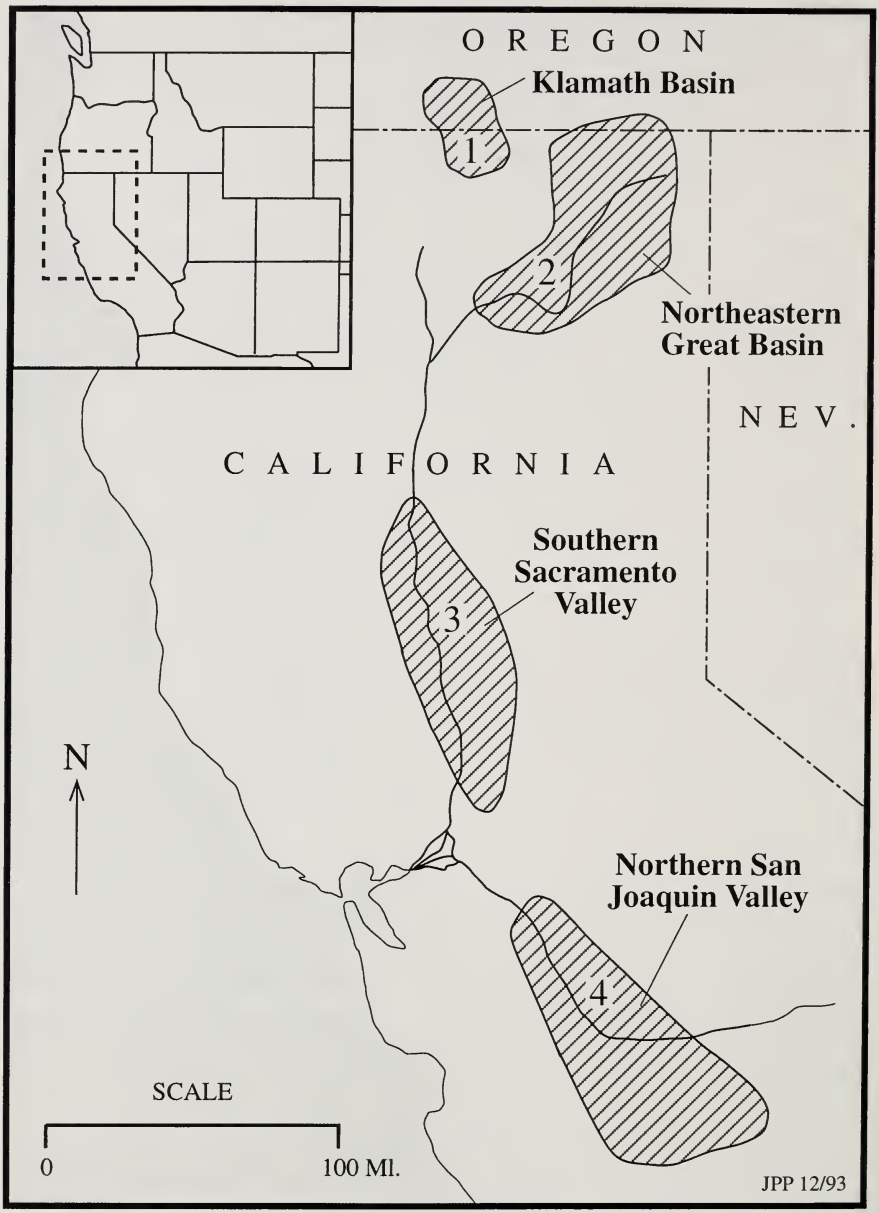

FIG. 1. Geographic locations in California used by Cackling Geese during the nonbreeding season. Specific locations in each area where most observation effort was concentrated are Tulelake National Wildlife Refuges (NWR) (1), Big Valley (2), Sacramento Valley NWRs (3), and Merced NWR (4).

We included a day in the analysis only when we had observed geese for >8 h. Observation effort in any one location in California was dictated primarily by movements of the geese (Johnson 1988, Raveling et al. 1992). During our study, Cackling Geese used the Klamath Basin (Fig. 1) between mid-October and early-December. Between early-December and mid-January, most Cackling Geese in California were found in the Sacramento and San Joaquin valleys. After mid-January and before their departure in late-April for Alaska, Cackling Geese moved to the San Joaquin Valley, Big Valley, or Klamath Basin. Thus, comparisons of these four locations in California includes a seasonal component.

Two observers in 1989 and three observers in 1990 observed Cackling and Ross' geese in Big Valley on a daily basis between 1 March and their respective departures in mid- and late-April. An observation day was included in the analysis only if geese were followed from dawn until dusk. When a goose flock flushed, we recorded the probable cause of the flush. We assumed an eagle caused the flush if we observed an eagle flying in the area and if the direction of the initial flush was away from the direction of the eagle. We recorded the date, time, and location of all eagle-associated flushes, attacks, and kills. An eagle attack was designated only when an eagle stooped and/or chased geese. In addition, whenever a goose flock was flushed by an eagle we estimated the size and species composition of the flock.

California Dept. of Fish and Game (CDFG) biologists coordinated counts of Bald Eagles throughout California during mid-January 1979–1981 and from 1986 to the present (Detrich, unpubl. data; Nahstoll, unpubl. data). We used these counts to estimate general distribution and population trends of Bald Eagles during our study. We used counts of Golden Eagles recorded during the mid-January Bald Eagle survey as an indication of the relative occurrence of Golden Eagles in specific geographic locations in California.

Because geese concentrated in and around refuges, we also used eagle population estimates made by biologists at Sacramento National Wildlife Refuges (specifically Sacramento, Delevan, and Colusa NWR) and at Klamath Basin National Wildlife Refuges (specifically Lower Klamath and Tulelake NWR). Biologists at both refuge complexes conduct bimonthly surveys of all waterfowl species and eagles. In addition, raptors at Tulelake and Lower Klamath NWR are censused bimonthly from 1 October–30 April along a series of transects established in 1985. In the results, we specify whether we are using the mid-January counts, bimonthly surveys, or bimonthly transect counts to estimate eagle numbers, or the proportion of Bald/Golden eagles in the population.

We used *G*-tests (Sokal and Rohlf 1981) for testing hypotheses about frequencies of eagle attacks and flushes in Big Valley in different habitats and across the daily period. The expected frequency distribution for testing habitat-related patterns in eagle attacks and flushes was determined by dividing the area of each goose habitat type by the total area used by the geese. These proportions are: day roost (0.046), pasture (0.597), alfalfa (0.139), wet meadow (0.140), and winter wheat (0.078). The expected frequency distribution for testing daily patterns in eagle attacks and flushes was determined by dividing the duration of each of the three time periods by the total time spent watching geese per day. These proportions are: morning (0.286), mid-day (0.428), and evening (0.286).

In 1989, we watched geese for similar amounts of time on all habitats except for winter wheat (day roost/wet meadow = 116 h, pasture = 113 h, alfalfa = 108 h, winter wheat = 32 h). In 1990, we spent more time watching geese on wet meadow and alfalfa (day roost/wet meadow = 270 h, pasture = 114 h, alfalfa = 194 h, winter wheat = 42 h). Consequently, prior to statistical analysis, we expressed all habitat-related patterns in eagle attacks and flushes per 100 hours of observation basis. Whenever expected values for one of the two years was less than 10, we pooled frequencies for both years.

We compared sizes of goose flocks flushed by eagles on four feeding habitats and the

TABLE 1

FREQUENCY OF EAGLES KILLING CACKLING GEESE AND MID-JANUARY POPULATION ESTIMATES OF BALD EAGLES AT SELECTED WINTERING LOCATIONS IN CALIFORNIA

Location and year	No. obs. days	Golden Eagle		Bald Eagle		No. Bald Eagles in mid-Jan.
		Kills	Predation rate[a]	Kills	Predation rate[a]	
Klamath Basin						
Oct.–Dec. 1985	47	2	1.3	1	0.6	109
Oct.–Dec. 1986	78	6	2.3	2	0.8	130
Oct.–Dec. 1987	30	10	10.0	0	—	965
Sacramento Valley						
Nov. 1985–March 1986	58	0	—	0	—	No count[b]
Nov. 1986–March 1987	51	1	0.6	0	—	9
Nov. 1987–March 1988	23	0	—	0	—	4
San Joaquin Valley						
Feb.–April 1986	42	0	—	0	—	Poor count[b]
Feb.–April 1987	35	1	0.9	0	—	3
Feb.–April 1988	11	0	—	0	—	3
Big Valley						
March–April 1989	38	2	1.6	0	—	7
March–April 1990	50	3	1.8	0	—	6

[a] No. of eagle kills observed divided by number of observation days × 30 days.
[b] Caused by extensive fog during count period.

day roost in Big Valley for 1989 and 1990 using an unbalanced design analysis of variance (ANOVA) (Sokal and Rohlf 1981). If we observed a flock of geese flushed more than once by eagles at the same location on the same day, we used the average flock size for that day in the analysis. The flock size data conformed to the assumptions of ANOVA.

RESULTS

Large-scale spatial and temporal variation in eagle predation.—Eagles were observed killing Cackling Geese on average once every three days in the Klamath Basin, but the frequency of eagle kills varied annually (Table 1). Only one eagle kill was seen in 132 observation days in Sacramento Valley and 88 observation days in the San Joaquin Valley. In Big Valley, eagles were observed killing Cackling Geese every 17–19 days on average. Golden Eagles were responsible for 89.3% of all Cackling Goose kills observed. Bald Eagles were observed killing Cackling Geese only in the Klamath Basin where they were responsible for 14% of all eagle kills observed. We observed an immature eagle attacking and killing a Cackling Goose only once.

The Klamath Basin contained over 10 times more Bald Eagles, in any

given year, than the other three locations where Cackling Geese congregated (Table 1). Golden Eagles in northeastern California represented 26–51% of the total number of Golden Eagles observed in California during the mid-January surveys in 1979–1981, whereas the Central Valley of California (including Sacramento and San Joaquin valleys) contained only 9–11% of all Golden Eagles observed (Detrich, unpubl. data). Unfortunately, few observations of Golden Eagles have been reported during the mid-January surveys since 1981. Big Valley had 6–7 Bald Eagles (Table 1) and probably 3–4 Golden Eagles (McWilliams, pers. obs.) in 1989 and 1990, making it second only to the Klamath Basin in eagle population density.

Annual changes in Bald Eagle populations were most evident in the Klamath Basin (Table 1), where nearly 1000 wintering eagles were observed in 1987. Despite this large concentration of Bald Eagles, more geese were killed by Golden Eagles than by Bald Eagles in 1987 (Table 1). Based on the raptor transect counts at Tulelake NWR, 1.5%, 3.0%, and 0.8% of eagles were identified as Golden Eagles in 1985, 1986, and 1987, respectively. Applying these percentages to the bimonthly aerial counts of eagles at Tulelake NWR, we estimated between one and eight Golden Eagles were present each fall, 1985–1987.

We observed eagles killing Cackling Geese within two days of their arrival in the Klamath Basin and at least one month prior to peak eagle populations (Fig. 2). During fall 1985, we saw three Cackling Geese killed by eagles. All three geese were killed soon after most Cackling Geese had arrived in the Klamath Basin and when Cackling Geese were most abundant. During fall 1986, we saw six Cackling Geese killed by eagles. Five of the six geese were killed during the approximately 25-day period when Cackling Geese were arriving in the Klamath Basin and when they were most abundant. During fall 1987, eagles killed 10 Cackling Geese in 10 days. During these 10 days, most Cackling Geese arrived in the Klamath Basin and peak counts of Cackling Geese were recorded.

The pattern of eagle predation on Cackling Geese was also related to the availability of alternative prey. During fall 1985, we saw no Cackling Geese killed by eagles after white geese arrived in the Klamath Basin. After white geese arrived in the Klamath Basin in fall 1986, we observed only one eagle kill a Cackling Goose even though Cackling Goose abundance remained relatively high during November and December (Fig. 2). During fall 1987, there were more Cackling Geese than in 1985 and 1986 and white geese never were abundant. We observed more Cackling Geese killed by eagles in fall 1987 than in fall 1985 and 1986.

Geese crippled or killed by hunters may provide more susceptible prey for eagles and thus reduce eagle attacks on healthy geese. If carrion avail-

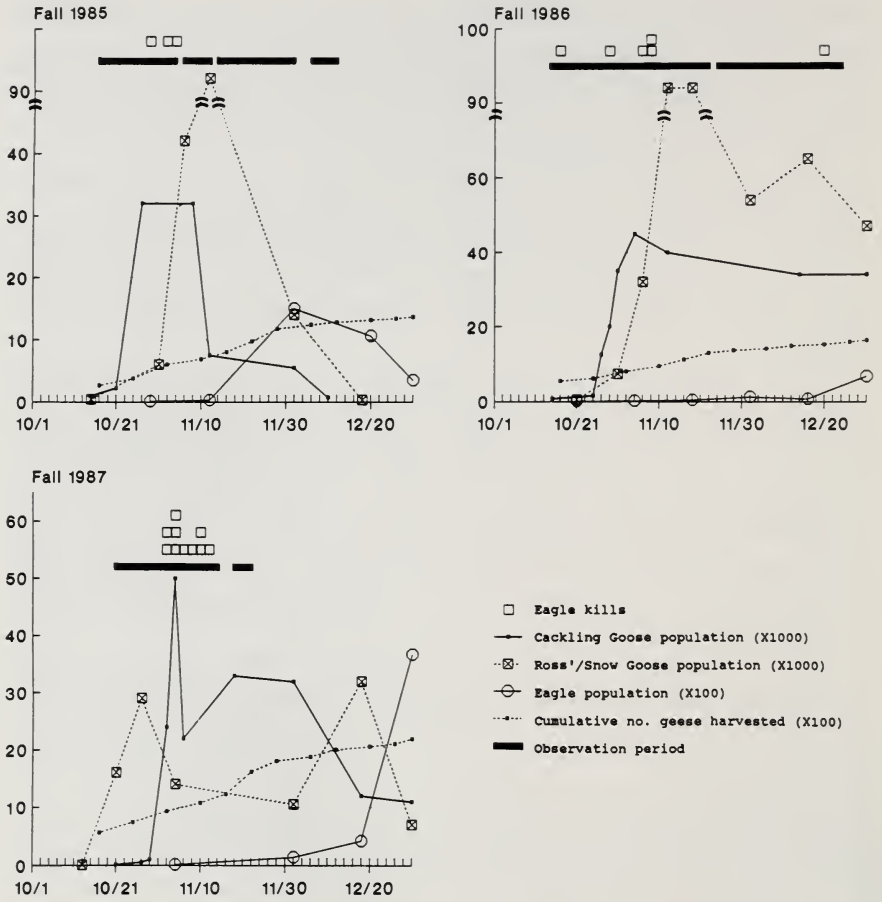

FIG. 2. Possible factors which influence the temporal pattern of eagles killing Cackling Geese during fall, 1985–1987, at Tulelake NWR, CA. Cackling Goose population estimates are based on our counts. White geese (Ross' and Lesser Snow geese) and eagles were counted during bimonthly aerial censuses conducted by Tulelake NWR personnel. Goose harvest data was also collected by Tulelake NWR personnel. Observation period includes all days when at least eight hours per day were spent observing geese.

able to eagles is directly proportional to the number of geese shot by hunters, then almost twice as many geese were available as carrion in 1987 compared to 1985 and 1986 (Fig. 2). In 1987, we saw no Bald Eagles kill a Cackling Goose, while Golden Eagles preyed heavily on Cackling Geese (Table 1).

Spatial and temporal changes in eagle predation in Big Valley.—In both 1989 and 1990, the rate of eagle-caused flushes in Big Valley was

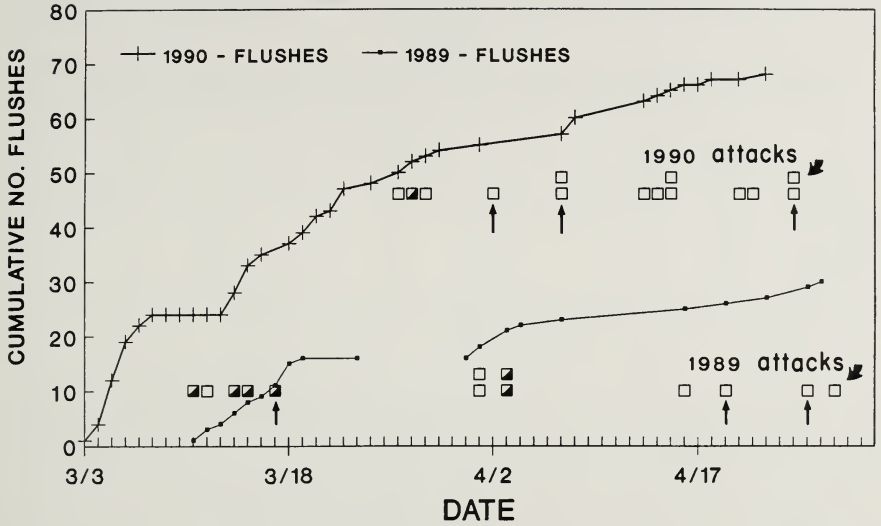

FIG. 3. Temporal patterns of eagle-caused flushes, eagle attacks, and eagle kills of geese in Big Valley, California during March and April, 1989 and 1990. Unshaded squares denote days eagles attacked Cackling Goose flocks. Half-shaded squares denote days eagles attacked mixed Ross'/Cackling goose flocks. Arrows denote attacks which resulted in a goose being captured by the eagle.

highest just after arrival of the geese (2.1 flushes/day between 11–19 March in 1989, 5.0 flushes/day between 3–7 March in 1990), and then declined to 0.4 flushes/day between 3–25 April in 1989 and 0.7 flushes/day between 25 March–24 April in 1990 (Fig. 3). The rate of eagle-caused flushes was consistently higher in 1990 than in 1989. In 1989, 36% of eagle attacks occurred during the time when the rate of eagle-caused flushes was highest. In 1990, all eagle attacks occurred during the period when eagle flush activity was at its lowest rate.

In 1989 and 1990, we observed 62% and 43%, respectively, of eagle-caused flushes during mid-day (Table 2). Eagle attacks in 1989 occurred primarily during mid-day or evening periods, whereas in 1990 most eagle attacks occurred during the evening period. When differences in the amount of observation time for each time-of-day period were considered for both years, the frequency of eagle flushes did not vary across the daily period ($G = 1.75$, $P > 0.05$), but the frequency of attacks was higher in the evening ($G = 8.62$, $P < 0.05$).

More eagle-caused flushes occurred on day roost site(s) than expected (Table 3, total for both years), based on its proportion of the total area ($G = 116.8$, $P < 0.01$). However, frequency of eagle attacks on the day

TABLE 2

FREQUENCY WITH WHICH CACKLING AND ROSS' GEESE WERE FLUSHED, ATTACKED, AND KILLED BY EAGLES DURING THREE DAYTIME PERIODS IN BIG VALLEY, CALIFORNIA

Time-of-day[a]	1989			1990			Total		
	Flushes	Attacks	Kills	Flushes	Attacks	Kills	Flushes	Attacks	Kills
Morning	4	2	0	22	3	0	26	5	0
Mid-day	20	6	2	30	1	1	50	7	3
Evening	8	5	1	18	10	2	26	15	3

[a] Morning = 06:00–10:00 PST, Mid-day = 10:00–16:00 PST, Evening = 16:00–22:00 PST.

roost or on any feeding site was not different than expected ($G = 7.31$, $P > 0.05$). Geese typically used the day roost between 10:00–16:00 h PST, spending most of this time resting on the water or shore. However, portions of the mid-day period were usually spent feeding in wet meadows adjacent to the day roost. When the relative sizes of habitats used by feeding geese were considered, comparisons of only feeding sites revealed differences in eagle-caused flushes ($G = 26.7$, $P < 0.01$) but no differences in eagle attacks ($G = 0.78$, $P > 0.05$). Five of the six geese killed by eagles occurred while geese were feeding on either pasture or wet meadow sites.

If expected values were calculated assuming equal likelihood of attacks or flushes in each feeding habitat, the frequency of flushes was higher in pasture and wet meadow ($G = 8.99$, $P < 0.05$) and the frequency of attacks was higher in pasture ($G = 9.35$, $P < 0.05$) compared to other habitats where geese fed.

Predation pressure differences for sympatric geese.—In 1989 and 1990, we observed seven and 13 eagle attacks, respectively, on pure

TABLE 3

FREQUENCY WITH WHICH CACKLING AND ROSS' GEESE WERE FLUSHED, ATTACKED, AND KILLED BY EAGLES WHILE ON THE DAY ROOST OR ON SPECIFIC FORAGING HABITATS IN BIG VALLEY, CALIFORNIA

Habitat	1989			1990			Total		
	Flushes	Attacks	Kills	Flushes	Attacks	Kills	Flushes	Attacks	Kills
Day roost	14	4	1	46	2	0	60	6	1
Wet meadow	4	1	1	8	3	2	12	4	3
Pasture	10	6	1	6	6	1	16	12	2
Alfalfa	1	1	0	6	3	0	7	4	0
Winter wheat	3	1	0	2	0	0	5	1	0

TABLE 4
FREQUENCY OF GOLDEN EAGLE ATTACKS AND KILLS FOR CACKLING, ROSS', AND GREAT BASIN CANADA GEESE IN BIG VALLEY, CALIFORNIA

Goose species	1989			1990		
	Attacks	Kills	Predation rate	Attacks	Kills	Predation rate
Cackling	7	2	10.3[a]	13	3	8.4[b]
Ross'	0	0	5.3[c]	0	0	0.8[d]
Cackling and Ross'[e]	6	1	—	1	0	—
Great Basin	1	0	0.8[f]	0	0	0

[a] (13 attacks/38 obs. days) × 30 days.
[b] (14 attacks/50 obs. days) × 30 days.
[c] (6 attacks/34 obs. days) × 30 days; all attacks were on mixed flocks.
[d] (1 attack/40 obs. days) × 30 days; all attacks were on mixed flocks.
[e] Mixed species flocks.
[f] (1 attack/38 obs. days) × 30 days.

Cackling Goose flocks and no eagle attacks on the relatively rare pure Ross' Goose flocks (Table 4). Of the 20 observed eagle attacks on pure Cackling Goose flocks, 20% resulted in a Cackling Goose being caught and killed by an eagle. Of the seven observed eagle attacks on mixed Ross' and Cackling Goose flocks, only one Ross' Goose was killed. Eagles attacked mixed species flocks as often as pure Cackling Goose flocks in 1989 (6 of 13 attacks) but usually attacked pure Cackling Goose flocks in 1990 (13 of 14 attacks).

Cackling Geese were attacked by eagles an average of once every 3–4 days whereas Ross' Geese were attacked by eagles an average of once every 6–40 days (Table 4). We observed only one Golden Eagle attack on a Great Basin Canada Goose (Table 4).

Risk of eagle predation and the responses of geese.—In Big Valley, eagles attacked goose flocks of many sizes (Fig. 4). Flocks larger than 3000 geese were frequently flushed by eagles, but were less commonly attacked than smaller flocks. Eagles flushed larger flocks of geese on the roost site than on the four feeding habitats (Table 5; $F_{4,73} = 9.22$, $P = 0.0001$). In both 1989 and 1990, the predation risk experienced by an individual goose on a given habitat was highest when it was in a pasture (Table 5). Feeding geese typically spent 15–35% of the time with their heads up scanning for predators. Time spent vigilant was not significantly different across habitats (McWilliams and Raveling 1994).

Cackling and Ross' geese always responded to eagle attacks by flushing into the air. If geese were on water prior to the attack, they often circled in tight, compact flock(s) 30–200 m above the water. If the eagle persisted, the flock would usually become divided and the geese would try

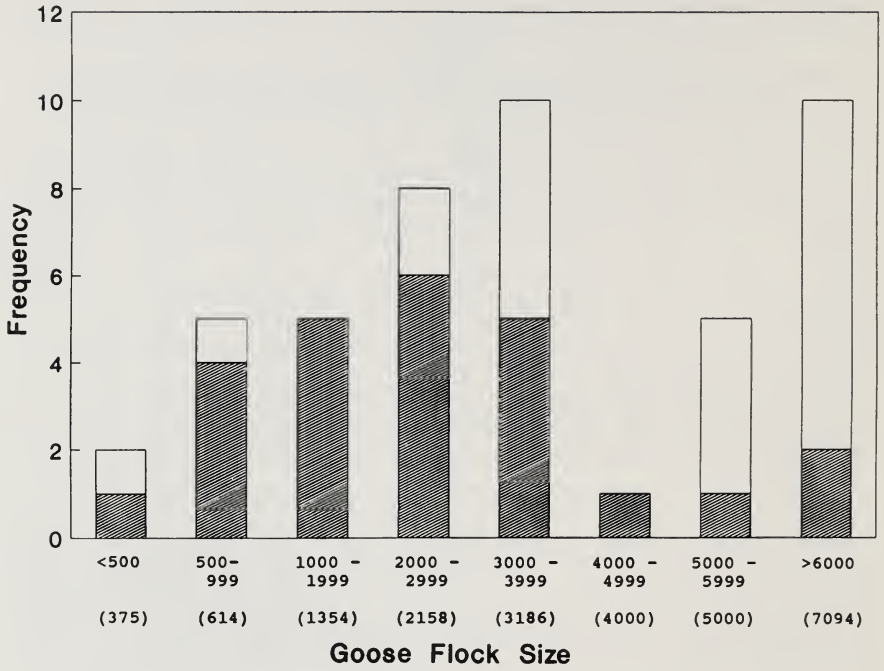

FIG. 4. Frequency distribution of goose flock sizes that were flushed or attacked by Golden Eagles in 1989 and 1990. One entire bar represents the number of flushes observed for a given flock size, and the hatched portion of each bar shows the number of flushes which escalated into attacks. Numbers in parentheses are the average flock size for each flock size class.

to outdistance the eagle by flying off as quickly as possible. While Cackling and Ross' Geese were flying about, Great Basin Canada Geese on the same field usually remained on the ground. The only eagle attack on a Great Basin Canada Goose that we observed involved a Golden Eagle grabbing the back of the goose. The goose then grabbed the eagle with its bill and hit the eagle with its wings. The eagle left within five min of initiating the attack and the goose suffered no apparent lasting effects.

DISCUSSION

Eagle/goose interactions at large and small spatial scales.—In general, geographic variation in the frequency of eagle predation on geese is best explained by patterns of eagle abundance. Of the 28 Cackling Geese we observed killed by eagles during 1985–1990, 93% were observed in northeastern California (including both Klamath Basin and Big Valley). Currently, the Klamath Basin supports the largest concentration of win-

TABLE 5

COMPARISON OF TIME SPENT VIGILANT, AVERAGE FLOCK SIZE, AND PREDATION RISK FOR CACKLING AND ROSS' GEESE AT THE DAY ROOST AND IN FOUR HABITATS COMMONLY USED WHILE FEEDING IN BIG VALLEY, CALIFORNIA

	Percent time vigilant[a]				Flock sizes flushed by eagles						Predation risk[b]	
	1989		1990		1989			1990				
Habitat	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	N	$\bar{x}$	SE	NE	1989	1990
Day roost	—	—	—	—	5536	680	14	4360	381	30[c]	7.2	4.6
Wet meadow	33	11	26	12	4625	375	4	2007	267	7[c]	2.2	14.9
Pasture	27	15	27	11	2125	555	10	1783	322	6	28.2	33.7
Alfalfa	26	14	16	10	1600	—	1	1933	81	6	6.3	15.5
Winter wheat	18	9	15	8	3467	1533	3	750	250	2	8.7	—

[a] Calculated from McWilliams and Raveling (1994); vigilance = % time with head above horizontal plane of back.

[b] Predation risk = (no. eagle attacks/mean flock size) × 10,000. Mean flock sizes used are those given above. Frequency of eagle attacks per habitat is from Table 3.

[c] Samples sizes are different than those in Table 3 because we did not always estimate goose flock size during an eagle attack or because, prior to ANOVA analysis, we averaged flock sizes flushed by eagles at the same location on the same day.

tering Bald Eagles in the contiguous U.S. (Palmer 1988a), along with impressive concentrations of over one million waterfowl (Keister et al. 1987). In some years, Golden Eagles are also more abundant in northeastern California than at other locations used by Cackling Geese, although population estimates for Golden Eagles in California are lacking. There is no evidence that geese respond to this large scale variation in eagle activity. Johnson (1988) found no significant differences in time-activity budgets of Cackling Geese in Klamath Basin, Sacramento or San Joaquin valley, or Big Valley during winter 1982–1983 and 1983–1984.

Once flocks of geese have at least 200 individuals, the time spent vigilant by individuals no longer decreases (Lazarus 1978, Inglis and Lazarus 1981). This may explain why Cackling Geese in Big Valley were not more vigilant in habitats with higher risk of predation. Small birds which live in small flocks (<20 birds) respond to increased predation risk by increasing group size (Caraco et al. 1980). In contrast, we found that although geese encountered spatial variation in predation risk, geese remained in flocks of about 2000 individuals across habitats. We suspect that flock size of Cackling and Ross' geese is dictated primarily by the distribution and abundance of food plants and by the local population size of geese, with some minimum flock size threshold determined by risk of predation. The fact that flock sizes were largest on the day roost where feeding does not occur suggests that some constraint(s) associated with feeding limits flock size in Cackling and Ross' geese.

Eagle/goose interactions at large and small temporal scales.—In the Klamath Basin, Cackling Geese were attacked by eagles more often in years when populations of Cackling Geese were large and when Cackling Geese stayed longer. Moreover, eagles reduced their hunting of Cackling Geese when white geese were more abundant than Cackling geese. These predation patterns suggest that Golden and Bald eagles feed disproportionately on the most abundant prey and that changes in the availability of alternative preferred prey influenced the pattern of eagle predation (also see Steenhof and Kochert 1988). The lack of a relationship between Bald Eagle population and frequency of eagles killing Cackling Geese is not surprising because the large concentrations of wintering Bald Eagles in the Klamath Basin feed primarily on scavenged waterfowl (Frenzel and Anthony 1989).

Eagles killed Cackling Geese most frequently 1–10 days after Cackling Geese arrived in the Klamath Basin each year. In Big Valley, we also observed more eagle/goose interactions soon after arrival of the geese. Geese may be more vulnerable to eagle predation on or after long migrations because of exhaustion (Ogilvie 1978:177), because they must spend more time eating to meet nutrient demands (Sedinger and Bollinger 1987, Raveling and Zezulak 1991) and are consequently less vigilant, or perhaps because they must learn that particular locations are more risky.

At all wintering locations in California, Cackling and Ross' geese traditionally spend the mid-day period on water at a roost site. When geese were on the day-roost in Big Valley, they experienced significantly more eagle-caused flushes but similar frequencies of attacks compared to habitats where geese fed. It appears the large mid-day concentration of roosting geese effectively reduced eagle predation attempts.

Nature of eagle/goose predator-prey relations.—Reports of Bald Eagles capturing birds as large as geese in flight are rare (e.g., Rudebeck 1950, 1951; Bennett and Klaas 1986; Nero 1987; Bartley 1988) and reports for Golden Eagles rarer still (see Palmer 1988b). Eagles adopt a variety of strategies when hunting geese, with ground attacks and stoops (Stalmaster 1987, Palmer 1988a, b) being the most common methods employed. All successful attacks we observed involved the eagle grabbing the back of the goose and then gliding to the ground. This type of capture is unlike that described by Brewster (1880), Herrick (1934), and Stalmaster (1987) in which the Bald Eagle grabbed the belly of the goose as the eagle performed a somersault maneuver. An element of surprise is a common feature of the eagle's hunting methods. The primary antipredator strategy of geese includes aggregation and early detection through vigilance combined with aerial escape. Cackling and Ross' geese used so-

cially-coordinated and speed-based tactics during aerial escape (after Lima 1993).

Body size differences between Great Basin Canada and Cackling geese strongly influenced the frequency of predation by eagles. Snow Geese, an intermediate-sized goose, are preyed on by eagles only rarely (Rudebeck 1950, 1951; Bennett and Klaas 1986; Nero 1987; Bartley 1988). The various species and subspecies of geese form a continuum of body sizes that includes the size threshold above which eagles apparently prefer not to attack. Probably in response to increased predation risk, the smaller body-sized geese occur in denser flocks and consequently have reduced family cohesiveness (Johnson and Raveling 1988). Whether predation alone is responsible for the evolution of this behavior is unlikely, because flocking in geese may also have important feeding advantages (Owen and Black 1990).

Ross' and Cackling geese are similar in size, but Cackling Geese were attacked and killed at least twice as often as Ross' Geese in Big Valley. We suggest this interspecific difference in frequency of predation occurs primarily because Cackling and Ross' geese have different foraging strategies. Both Cackling and Ross' geese graze in similar habitats, but the two species differ in the proportion of time spent on specific habitat types (McWilliams and Raveling, in press). Cackling Geese spent 16–52% ($\bar{x}$ = 34%) of their foraging time during March and April on pasture where eagles are more active, whereas Ross' Geese spent 0–15% ($\bar{x}$ = 4%) of their foraging time on pasture.

An alternative explanation for the higher rate of predation on Cackling Geese is that eagles simply prefer Cackling Geese and consequently follow them to their feeding sites. We believe this is less likely because, compared to other sites where geese fed in Big Valley, pasture areas had more Belding and California ground squirrels (*Citellus beldingi* and *Otospermophilus beecheyi*) and black-tailed jackrabbits (*Lepus californicus*) which are the most frequent prey of Golden Eagles in northeastern California (Bloom and Hawks 1982).

Predator-prey systems, like the eagle-goose system we have analyzed, are probably often strongly influenced by the predatory behavior of individuals (Rudebeck 1950, 1951; Page and Whitaker 1975; Palmer 1988a, b). All six successful eagle attacks on geese that we observed in Big Valley were made by a single adult male Golden Eagle identifiable by a white wing patch (see Jollie 1947:572). This one eagle was not responsible for the majority of eagle-caused flushes, but was responsible for the majority of eagle attacks on goose flocks.

In summary, we found that spatial and temporal variation in eagle predation on Cackling Geese was related to variation in the abundance

and distribution of eagles, geese, and alternative prey. Geese did not modify their vigilance time or flock size in response to spatial and temporal variation in predation risk. Interspecific differences in the susceptibility of geese to eagle attacks were strongly influenced by the body size and foraging strategy of the geese. Cackling Geese reduced the risk of eagle predation by occurring in large, dense flocks, detecting eagles through vigilance, and by resting with many other geese in locations which provided some protection from eagles.

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CHICK MOVEMENTS AND ADOPTION IN A COLONY OF BLACK-LEGGED KITTIWAKES

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ABSTRACT.—We studied Black-legged Kittiwakes (*Rissa tridactyla*) in an Alaskan colony where movement of young among nests was possible because of moderate terrain and close nest spacing. Thirty-three percent of chicks in a focal group departed their nests prior to fledging, and seven of the vagrant chicks (58%) were adopted by foster parents. The overall frequency of adoption in three years was 8% of 88 chicks from 57 focal nests. Premature nest-departure occurred at different stages among first- and second-hatched chicks. Departing second-hatched chicks were usually expelled by their nest mates within a few days after hatching. First-hatched chicks left at all stages and usually were the sole nest occupant when they departed. The evidence for parent-offspring recognition was equivocal. Adults accepted alien chicks that appeared in the nest and also occasionally attacked their own young outside the nest. However, asymmetry in the response of parents and nonparents to vagrant chicks seeking access to a nest suggested that adults were often able to discriminate appropriately. Vagrant chicks appeared to have little control over their fate—most entered nests where they were smaller than the resident young and suffered nest-mate aggression. Reproductive error seems the likely explanation for the acceptance and foster caregiving observed in adult kittiwakes. *Received 26 Jan. 1993, accepted 18 Sept. 1993.*

Foster parenting appears to be a fairly common phenomenon in colonial ground-nesting gulls and terns (e.g., Holley 1981, Carter and Spear 1986, Pierotti and Murphy 1987, Morris et al. 1991). The young of these species leave their nests within a few days after hatching and wander freely over their own and occasionally over neighboring territories. Such predisposing factors result in reported adoption rates of 2–15% per nest among *Larus* gulls, depending on the species and habitat (Hébert 1988). In contrast to their ground-nesting relatives, Black-legged (*Rissa tridactyla*) and Red-legged (*R. brevirostris*) kittiwakes typically nest on narrow cliff ledges. Chicks ordinarily remain within the immediate confines of the nest until they are able to fly, which minimizes the possibility of brood mixing and adoption. Nest area confinement may also account for a reported absence of parent-offspring recognition before fledging (Cullen 1957). There is, however, one account of naturally occurring adoptions in Black-legged Kittiwakes (Pierotti and Murphy 1987), and in food-stressed colonies it is not uncommon for young to leave the nest prematurely because of sibling rivalry (Braun and Hunt 1983).

We studied Black-legged Kittiwakes in a colony where chick mobility outside the nest was not restricted greatly. We observed considerable

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(a)

(b)

(c)

chick movement among nests, involving young of widely varying age and size. Our aim in this paper is to document the frequency and circumstances of premature nest-leaving in kittiwakes and to revisit the issue of parent-offspring recognition in this species.

METHODS

Middleton Island (north-central Gulf of Alaska, 58°25′N, 146°19′W) supports a large but declining colony of Black-legged Kittiwakes (ca 39,000 pairs in 1991; Hatch et al. 1993a). We used two study plots there for observations in three years (Plot B [1984 and 1985] and Plot C [1988]). The plots were situated about 150 m apart on a low bluff on the northeast side of the island. Whereas kittiwakes commonly nest on the narrow ledges of sheer cliffs, our plots were characterized by moderately sloping terrain and close, relatively uniform nest spacing (Fig. 1).

Productivity was generally low on Middleton (0.76, 0.04, and 0.21 chicks per nest, island-wide, in 1984, 1985, and 1988, respectively; Hatch et. al. 1993b) and most of the nests observed on the behavior plots failed each year. Because of the similar outcomes and small samples in some instances, data from all three years are combined for describing patterns of chick movement and adoption in this colony.

Plots were observed throughout chick-rearing (about 25 June to mid-August) using a 15–60× spotting scope from below Plot B (1984–1985) or binoculars from the bluff above Plot C (1988). Samples of focal nests (15 nests each in 1984 and 1988, eight nests in 1985) in which one or both of the adults were individually color-banded were watched simultaneously, beginning between 06:00 and 08:00 ADT in the morning and ending between 20:00 and 22:00 at night. In 1984, breaks of 30–60 min occurred occasionally between observation shifts of 2–3 h. Observations were continuous in 1985 and 1988.

Chick losses reduced our sample of focal nests in 1984 and 1985. In 1988, we added new nests to the focal group, as required, to maintain an active sample of 15 nests under observation. In all, 34 different nests were closely observed during all or a portion of the chick-rearing period in 1988. Data from the focal nests were supplemented with less intensive observations on nonfocal nests in 1985 (46 additional nests on Plot B) and 1988 (125 additional nests on Plot C). The contents of nonfocal nests were checked a minimum of once daily, which allowed us to detect some chick movements when the event itself was not actually observed. For instance, if a nonfocal nest that previously contained two chicks had three chicks, we assumed that a chick movement into that nest had occurred and made further observations on the behavior and fates of the individuals involved. Usually the alien chick could be distinguished from its nest mates by its markings, degree of feather growth, injuries, coloration, or obvious size differences in comparison to the resident chicks. We sometimes deduced the nest from which a chick had come by noting which nest in the vicinity had most recently lost a chick.

Mean clutch sizes were 1.9–2.0 eggs in the focal nests. In 1984, first and second-hatched chicks were distinguished by marking the head of the first chick hatched with picric acid. In later years, we assumed that the larger chick had hatched first (Braun and Hunt 1983), because eggs hatched asynchronously, usually 1–2 days apart.

←

FIG. 1. Characteristic nesting habitat of Black-legged Kittiwakes on the northeast side of Middleton Island: (a) Plot B, (b) Plot C, (c) detail of Plot C from the bluff top showing close nest spacing and moderate slope.

We defined a chick movement as any instance of a chick residing outside its nest cup for any period of time. Chicks that departed either re-entered their natal nest, entered a foster nest, or died outside of any nest. A chick that left a nest and unsuccessfully attempted to enter one or more other nests was considered to have made one movement. We considered a chick adopted if we observed it being fed on one or more occasions by a foster parent at a non-natal nest.

When a chick moved out of a nest, we recorded the date and time, the chick's age, nest type (natal or non-natal), nest contents, relative age (natal nests) or size (non-natal) of any chicks left behind, and categorized the cause of departure. Our categories included (1) nest-mate aggression—chick was observed being pecked by nest mate(s) immediately before leaving, was known to be a frequent victim of aggression, or showed tell-tale injuries on the head, (2) adult non-attendance—a chick not in the above category left its nest while both adults were away, (3) accidents—chick fell or was inadvertently knocked out of a nest by adult, (4) gull disturbance—chick evaded a foraging Glaucous-winged Gull (*Larus glaucescens*) by leaving its nest, (5) parent-following—parent walked out of the natal nest and chick followed, and (6) prefledging activity—non-flying movements by chicks ≥40 days old. If a chick departed and re-entered its natal nest repeatedly (up to 23 departures were recorded in the extreme case), we assigned a single, predominant (most frequently observed) category for the purpose of tabulating the causes of nest-leaving at natal nests.

When a vagrant chick attempted to enter a nest, we recorded the date and time, nest type (natal or non-natal), presence or absence of adult(s), and adult response (attack or passive) to the entering chick. If the chick gained access to the nest, we noted its size relative to other chicks present, the occurrence of nest-mate aggression, whether the vagrant chick was fed by adult(s), and the duration of its stay. We recorded the final fate of vagrant chicks and their foster nest mates, along with age and cause of the deaths observed.

In summarizing data on chick movements and adult-chick interactions, we computed frequencies based on either the number of chicks sampled or, where appropriate, on the total number of behavioral events observed. We employ statistical tests of association (*G*-tests; Sokal and Rohlf 1981) only in the former case, because observations of the latter type were not independent (i.e., some of the same chicks were involved in multiple events).

RESULTS

Frequency of premature nest-leaving.—Twenty-nine (33%) of 88 chicks in focal nests departed their natal nests prematurely (Table 1). Having left its natal nest, a chick typically continued to wander, making an average of 4.5 movements in and out of nests before its fate was determined (Table 1). The frequency with which chicks departed their natal nests depended on the interacting effects of chick age and status within the brood. Most second-hatched chicks either departed their natal nest or died within three weeks after hatching. Those that departed were rarely (8.3%) the sole occupant of the nest when they left (Table 1). In contrast, first-hatched chicks were likely to leave at any stage during chick-rearing (58% moved after 31 days of age), and they were usually (88.2%) the sole nest occupant when they departed.

Causes of premature nest-leaving.—The majority of wandering chicks less than three weeks old were judged to have left their natal or acquired nests because of aggression from nest mates (Table 2). Accidents (chicks

Table 1

Frequency of Prefledging Kittiwake Chicks Leaving Their Natal Nests and Number of Moves per Vagrant Chick[a]

Chick age (days)	First-hatched chicks			Second-hatched chicks			Movements per chick[b]
	No. chicks observed	No. leaving (%)	Sole occupants (%)	No. chicks observed	No. leaving (%)	Sole occupants (%)	
1–10	48	6 (12.5)	4 (66.7)	25	9 (36.0)	1 (4.0)	1.7 ± 0.14 (45)
11–20	23	5 (21.7)	5 (100.0)	6	2 (33.3)	0 (0.0)	4.5 ± 1.44 (15)
21–30	20	2 (10.0)	1 (50.0)	4	2 (50.0)	0 (0.0)	4.2 ± 1.02 (10)
31+	12	7 (58.3)	7 (100.0)	1	0 (0.0)	—	8.6 ± 2.31 (18)
Overall[c,d]	56	17 (30.4)	15 (88.2)	32	12 (37.5)	1 (8.3)	4.5 ± 0.80 (76)

[a] Frequencies calculated for chicks in focal nests only; movements per chick include information from non-focal nests.
[b] Mean ± SE; number of chicks in parentheses. Movements from natal and acquired nests included.
[c] Sample sizes do not sum to overall totals because not all chicks were observed through all stages of chick rearing. Overall estimates of nest-leaving frequency are minimum values for the same reason.
[d] *G*-tests of overall difference between first- and second-hatched chicks; % leaving, $G = 0.46$ (1 df, ns); % sole occupants, $G = 19.62$ (1 df, $P < 0.001$).

falling from nests) were also an important risk among the youngest chicks (<10 days old). As chicks aged, premature nest-leaving was more frequently ascribed to parental non-attendance. Again, hatching order was an important determining factor, as the majority of second-hatched chicks departed because of nest-mate aggression, whereas most first-hatched chicks departed because of parental non-attendance, accidents, or other factors (e.g., gull disturbance or parent-following).

Table 2

Apparent Reasons for Prefledging Kittiwake Chicks Leaving Their Natal Nests[a]

Chick attribute	Number (%) of chicks leaving and cause				Total chicks
	Nest mate aggression	Nest unattended	Accidents	Other[b]	
Age (days)					
1–10	17 (53.1)	1 (3.1)	9 (28.1)	5 (15.6)	32
11–20	2 (18.2)	6 (54.5)	1 (9.1)	2 (18.2)	11
21–30	1 (12.5)	4 (50.0)	1 (12.5)	2 (25.0)	8
31+	0 (0.0)	9 (60.0)	1 (6.7)	5 (33.3)	15
Hatching order[c]					
First	3 (8.8)	14 (41.2)	7 (20.6)	10 (29.4)	34
Second	16 (72.7)	1 (4.5)	3 (13.6)	2 (9.1)	22

[a] Data from focal nests and non-focal nests included.
[b] Includes gull disturbance, parent-following, and pre-fledging activity.
[c] Distribution of causes differs significantly between first- and second-hatched chicks ($G = 26.7$, 3 df, $P < 0.001$).

TABLE 3
ADULT RESPONSES TO VAGRANT KITTIWAKE CHICKS ATTEMPTING TO ENTER NESTS

Chick age (days)	Percent adult-chick encounters in which adult attacked[a]			
	Non-parent			
	Empty nests	Active nests[b]	Overall	Parent
1–10	66.7 (15)	32.2 (31)	46.9 (49)	0.0 (4)
11–20	33.3 (3)	21.4 (14)	23.5 (17)	5.3 (19)
21–30	100.0 (7)	28.6 (7)	66.7 (15)	0.0 (5)
31+	25.0 (12)	12.9 (31)	16.3 (43)	8.3 (36)

[a] Sample sizes (no. of encounters) in parentheses.
[b] Nests containing eggs or chicks.

Consequences of premature nest-leaving.—Fourteen (48.3%) of the 29 focal chicks that prematurely left their nests re-entered their natal nests after a mean absence of 1.9 ± 0.86 h (range 0.02–8.1 h). Six chicks (42.9%) that re-entered natal nests eventually fledged, while the remainder died. Chicks that departed, returned, and survived at their natal nests were all relatively advanced in age (five were >30 days old and the sixth was 26 days old) when they made their excursion.

Among vagrant chicks that did not return to their natal nests, 12 (80.0%) gained access to a non-natal nest, whereas three (20.0%) never entered any nest and died. Seven chicks that entered non-natal nests were fed by resident adults. Thus, the overall rate of adoption was 8.0% (seven of 88 focal chicks). None of the adopted chicks from focal nests fledged. Including records from nonfocal nests, we observed 13 adopted chicks, of which one (7.7%) fledged, 10 (76.9%) died, and the fates of two chicks (15.4%) were unknown.

Whereas seven (58.3%) of 12 focal chicks that gained access to a non-natal nest were fed, in our inclusive sample of focal and nonfocal nests, only 13 (10.5%) of 124 chick movements into non-natal nests resulted in adoption. Often when a chick entered a non-natal nest, it was attacked by the resident adult. That response bore little relation to the age of the alien chick but was more prevalent when the prospective foster parent had no nest contents of its own (Table 3).

Chicks gaining access to active non-natal nests were usually smaller than the resident chicks. They frequently suffered aggression from their acquired nest mates, especially when they changed nests at a young age (Table 4). When a chick gained access to a nest where the resident chicks were smaller than itself, it usually escaped any aggressive response from its acquired nest mates.

We saw a few instances of aggression by a parent toward its own

TABLE 4

PERCENTAGE OF MOVES INTO NON-NATAL NESTS RESULTING IN VAGRANT CHICKS SUFFERING NEST MATE AGGRESSION[a]

Chick age (days)[b]	Size of vagrant chick relative to resident chick(s)	
	Larger	Smaller
1–10	0.0 (2)	91.7 (24)
11–20	0.0 (1)	13.0 (23)
21–30	— (0)	42.9 (7)
31+	14.3 (14)	41.2 (17)

[a] Sample sizes (no. movements) in parentheses.
[b] Age of vagrant chick.

wandering chick when the latter attempted to re-enter its natal nest (Table 3). However, of 64 attempts by wandering chicks to re-enter their natal nests when a parent was present, 63 (98.4%) were successful. In all (focal and nonfocal nests combined), we saw 131 attempts by vagrant chicks to enter non-natal nests while adults were present. Ninety-nine such attempts (75.6%) were successful. The age of the vagrant chick had little influence—34 (63.0%) of 54 attempts were successful among chicks aged 1–10 days, as were 15 (88.2%) of 17 attempts from 11–20 days old, eight (53.3%) of 15 attempts from 21–30 days old, and 42 (93.3%) of 45 attempts among chicks older than 30 days. A vagrant chick attempting to enter a non-natal nest with no adult present invariably gained access (N = 54 movements observed).

The mean residence time of an adopted chick in its non-natal nest was 12.7 ± 2.8 days (N = 13). Residence times were shorter for chicks that did not receive care, averaging 5.2 ± 0.9 h (N = 172 visits observed). We saw one instance of an adopted chick attacking and ejecting a resident chick. The victim was smaller than the adopted chick, which itself later fell from its foster nest and died. An adopted chick ejected two other alien chicks at one nest, and the fate of a resident chick was unknown at one nest where the resident and adopted chicks were similar in size and, therefore, indistinguishable. In remaining cases of adoption, the resident chick eventually fledged (one nest), the resident chick failed but the alien chick died first (one nest), or the alien chick was the sole occupant when it was adopted (eight nests).

DISCUSSION

The incidence of adoption in kittiwakes (8% of chicks from 57 nests) was comparable to rates reported for other larids (Hébert 1988). The assumptions that adoption is rare and its associated selection pressures

are minimal in kittiwakes (Cullen 1957) should be reconsidered accordingly. To be sure, the habitat we observed on Middleton Island was unusual in the relative absence of physical barriers to chick movement. In a typical colony, many nests are isolated on small ledges, which precludes any excursions of young outside the nest. Often there are places where nests are grouped on larger ledges, however, and in that situation, the close nest spacing of kittiwakes may actually promote exchanges of vagrant chicks among nests. Pierotti and Murphy (1987) reported six adoptions among kittiwakes nesting in a typical cliff colony.

Although both members of a brood were inclined to wander from the nest, the circumstances in which that occurred clearly differed between first- and second-hatched chicks. In competition for limited food, disadvantaged younger chicks typically departed (or were ejected) as a result of sibling aggression (see also Braun and Hunt 1983, Roberts and Hatch 1993). First-hatched chicks departed at an older mean age. Many of their excursions were possibly only an expression of prefledging restlessness, although they tended to be linked with persistent absence of the adults. Almost invariably, a first-hatched chick leaving its nest had already exercised the option of driving off its younger and smaller sibling.

The evidence was equivocal regarding individual recognition of young by adult kittiwakes. Adults were seen to attack their own young outside the nest, but chicks that entered a foster nest while the adults were away were accepted. This suggests that kittiwakes "recognize" their brood primarily by location (Cullen 1957) and that selection has favored the decision rule, "always accept young you find in the nest" (Beecher 1988). There was, however, a large disparity between parents and non-parents in the occurrence of aggression toward wandering chicks and in the likelihood of a chick's gaining access to a nest with an adult present. If kittiwakes identify their young only by location, it is difficult to explain the generally passive response of parents toward chicks attempting to reenter their natal nests.

Not surprisingly, non-parents were more likely to attack in cases where the adult had no nest contents when a foreign chick arrived. In that case, the adult had a reasonably firm basis to "know" the chick was not its own. Nevertheless, most adoptions occurred in situations where the foreign chick was the sole dependent when it became established. The main problem a chick faced once it had gained access to a foster nest was not acceptance by the adults but attacks administered by its acquired nest mates. Thus, most wandering chicks made several moves before succumbing or finding a permanent home.

As an apparently altruistic behavior, adoption in gulls has been explained hypothetically on the basis of reciprocal altruism (Pierotti 1980,

1982), kin selection (Waltz 1981), or the possibility that foster parents gain valuable experience or future assurance of a breeding territory (Carter and Spear 1986). Alternatively, adoption can be viewed simply as a reproductive error that selection has been unable to eliminate (Riedman 1982, Holley 1984, Plissner and Gowaty 1988). Because an adopted chick clearly benefits from the behavior, it may be that strong selection for survival tactics among disadvantaged chicks primarily drives the system (Pierotti and Murphy 1987, Hébert 1988, Morris et al. 1991). In the colony we studied, there was little, if any, measurable cost to host young or foster parents associated with adoption, because food shortage and gull predation ensured that few chicks fledged in any case.

Among second-hatched chicks at least, we saw little evidence that disadvantaged young "elected" to leave their natal nest (Pierotti and Murphy 1987, Morris et al. 1991). Kittiwakes may differ from flat ground nesters in that respect. Most movements occurred when young chicks were effectively expelled by siblings or acquired nest mates. Nor did vagrant chicks appear to exercise any choice of potential foster nests or the relative size or their prospective nest mates (Pierotti and Murphy 1987, Hébert 1988). Being easier to reach, downslope nests were the usual targets. Otherwise, a chick's attempt to enter a foster nest seemed more or less directed at random (Holley 1988). Most vagrants ended up in sites where they were smaller than the resident chicks and thus were no better off than they had been at home. That outcome was likely because soliciting chicks were usually small, and potential foster nests with small chicks were well-guarded by adults. A chick had a better chance of entering an empty nest or a nest where the resident young was older, larger, and sometimes unattended (Roberts and Hatch 1993).

We view the possibility of simple reproductive error as the most parsimonious explanation of alloparental behavior in kittiwakes. The reluctance of adults to admit foreign chicks who approached while they were present argues against the idea that foster parents stood to benefit by adopting. We suggest that recently failed kittiwakes adopted chicks that appeared in their nests because they were hormonally conditioned for care giving (Emlen 1976, Plissner and Gowaty 1988) and because, on balance, selection has favored an inhibition against rejecting chicks that reside in the nest.

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DAY/NIGHT VARIATION IN HABITAT USE BY WILSON'S PLOVERS IN NORTHEASTERN VENEZUELA

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Abstract.—We quantify the temporal variation in day and night habitat use by Wilson's Plovers (*Charadrius wilsonia cinnamominus*) in the Chacopata lagoon complex, in northeastern Venezuela, during the non-breeding season. The overall (day + night) time spent by plovers on foraging habitats did not vary seasonally. However, the duration of their presence on foraging sites during daylight was very short from November to January, but was compensated by an increase during nighttime. The day and night distribution of plovers over the lagoon complex differed substantially. Wilson's Plovers were gregarious and roosted most of the time during daylight. After dusk, they left their diurnal roosts and repositioned themselves solitarily throughout the lagoon mudflats, or flew to their nocturnal individual roosts close to mangroves. They foraged during low tides, but never during the entire low-tide periods, neither during daytime nor during nighttime. The plovers spent more time on foraging sites during the first part of the night than thereafter, and on moonlit nights, although they often occurred on feeding habitats during moonless nights. This appears to be correlated with the observation that *Uca cumulanta,* their main prey, is active during this portion of the night and on moonlit nights. The main reason why Wilson's Plovers are largely nocturnal appears to be the avoidance of diurnal predators. *Received 14 May 1993, accepted 10 Sept. 1993.*

Morrier and McNeil (1991) documented seasonal variation in daily activity of a permanent resident race of the Wilson's Plovers (*Charadrius wilsonia cinnamominus*) which breeds on the coast of northern South America, including the coastal lagoons of Venezuela (Hayman et al. 1986, McNeil et al. 1990). Assuming that Wilson's Plovers were resting from dusk to dawn, daylight feeding alone seemed insufficient from November to March to counterbalance energy expenditure, suggesting that Wilson's Plovers foraged substantially during nighttime (Morrier and McNeil 1991).

In many colonial waterbirds and various waterfowl species, including shorebirds, foraging may take place partly or entirely at night (see McNeil 1991; McNeil et al. 1992, 1993). In shorebirds, most studies concern the temperate zone. Although data are scarce, there are indications that nocturnal foraging also occurs in tropical environments (see McNeil 1991, McNeil et al. 1992). There are two main hypotheses to explain why shorebirds forage at night: (1) the "supplementary hypothesis" which postulates that night feeding occurs when daytime feeding has been inadequate

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to meet the birds' energy requirements, and (2) the "preference hypothesis" which postulates that the birds prefer to feed at night because it provides the most profitable, or the safest, feeding opportunities (see review by McNeil 1991, McNeil et al. 1992).

The need for nocturnal foraging presumably varies seasonally with the seasonal variation of energetic requirements for molting and pre-migratory or pre-reproductive fattening. The only available data for tropical areas were provided for migratory species in southern Portugal (Batty 1991) and Mauritania (Zwarts et al. 1990). In addition, it is unknown whether shorebirds forage throughout the night, during the entire duration of the low-tide period, or during part of each? The only available data so far were provided by Zwarts (1990) for Mauritania. Some predominantly visual feeders such as plovers take advantage of moonlight to feed at night (see McNeil 1991, McNeil et al. 1992). However, there are indications that some plover species use sight as the major method for prey detection, even on dark nights (McNeil 1991, McNeil et al. 1992, Turpie and Hockey 1993), and have comparable feeding success (Turpie and Hockey 1993), while other species of plovers and other daylight sight feeders switch to tactile feeding or stop foraging when light intensity is very low and the visual detection of prey is impaired (McNeil and Robert 1988, 1992; Robert and McNeil 1989; McNeil et al. 1992).

In this paper, we quantify the seasonal variation during the non-breeding season in diurnal and nocturnal habitat use by Wilson's Plovers that reside and breed in northeastern Venezuela. We also examine the hourly variation in the time they spend on nocturnal foraging areas. Finally, we discuss the effects of moonlight and tidal cycle on the plovers' use of nocturnal foraging habitats.

STUDY AREA AND METHODS

We conducted this study from October 1991 to March 1992 in the Chacopata lagoon complex (10°41'N, 63°46'W) on the north side of the Araya Peninsula, State of Sucre, in northeastern Venezuela (Fig. 1). Most observations took place in a 2 km^2 area surrounding the Bocaripo lagoon (Fig. 1). We mist-netted plovers monthly at four sites on the Bocaripo study area (Fig. 1). Radio transmitters (BD-2G, Holohil Systems Ltd, Woodlawn, Ontario), weighing 2.8 g and having an individual frequency, were glued to the back of 15 birds, using cyanoacrylate Krazy Glue (Borden Company Ltd, Willowdale, Ontario) according to the method used by Perry et al. (1981). Transmitter mass represented roughly 5% of the birds mass (54.4 g; Morrier 1990). Transmitters had a potential field life of at least 50 days, and their minimal detection range exceeded 2 km in optimal conditions, with the use of portable receivers (TRX-1000S, Wildlife Materials Inc., Carbondale, Illinois) and three element miniature folding antennas. We concentrated on locating daytime roosts within the main study area of the Bocaripo lagoon, but also located daytime roosts elsewhere in the Chacopata lagoon complex (Fig. 1).

Each month, on an hourly basis, we registered the position of radio-tagged plovers by

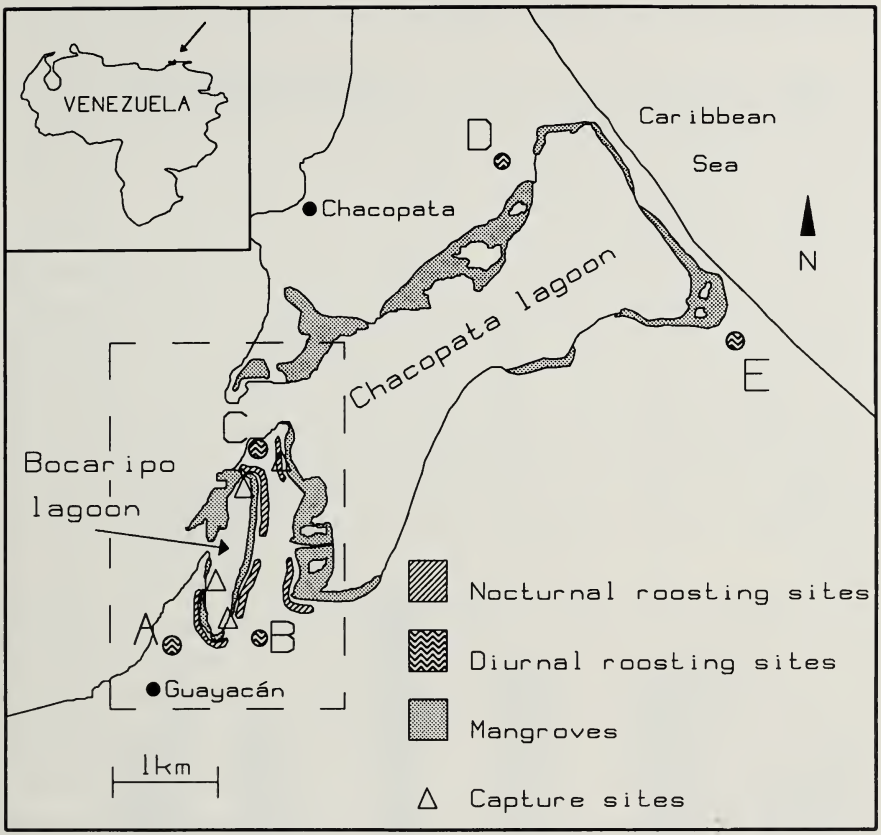

FIG 1. Map of the Chacopata lagoon complex in northeastern Venezuela. The main study area is delimited by a broken line.

using the triangulation method (see Heezen and Tester 1967) during at least five nocturnal and three diurnal periods, each lasting between 11 and 13 h, for a total of approximately 700 h of sampling. At night, we noted the relative size of the moon disc (moonless, quarter, half, or full moon); tide fluctuations were also noted on all occasions.

G-tests (Sokal and Rohlf 1981) were used to compare the percent of time spent by plovers on feeding habitats during daytime and nighttime, and to test the significance of seasonal variation in their hourly pattern of use of foraging areas during nighttime. A *G*-test for goodness of fit to a uniform distribution (Sokal and Rohlf 1981) was also computed to test the significance of the seasonal variation in the number of plovers observed at roost sites during daytime. The same test was also used to verify the significance of hourly variation in the presence of plovers on foraging habitats throughout the night and their relationship with the presence of moonlight and the tidal cycle. Finally, the presence of plovers on foraging sites during moonlit and moonless nights was compared with the Student *t*-test (Sokal and Rohlf 1981).

RESULTS

Diurnal and nocturnal distribution of plovers.—During daytime, from the end of October to March, Wilson's Plovers roosted on three sites (A, B, and C), 0.5 to 1.5 km apart, on the study area of the Bocaripo lagoon (Fig. 1). Site A, located near the village of Guayacán, was a rocky jetty, one meter in height, protecting the village from spring-tides. Site B was situated on the mudflat, beyond the maximum high tide limit on the mudflat, close to xeric vegetation. Site C was a shell (oysters and clams) heap exceeding in height the high tide level. Two other roosting sites were found outside the Bocaripo study area (Fig. 1), one near mangroves (site D), the other on the mudflat (site E), north and south-east of the Chacopata lagoon, respectively. From November to January, the plovers of sites D and E progressively decreased in number and disappeared. The number of Wilson's Plovers observed on sites A, B, and C varied significantly ($G = 20.44$, df = 5, $P < 0.01$) (numbers = 61, Oct. 1991; 101, Nov. 1991; 113, Dec. 1991; 91, Jan. 1992; 86, Feb. 1992; 71, March 1992).

The nocturnal and diurnal distribution of individual Wilson's Plovers differed substantially (Fig. 1). Telemetry revealed that the birds moved more at night than during daylight. For example, starting in November, one individual began to use site B during daytime and regularly moved at night to foraging sites by the Chacopata lagoon where it had previously been captured and radio-tagged. After the end of the transmitter field life, it was frequently observed roosting during daytime at the same site until the end of March, just before the beginning of breeding activities, when the daytime roosting groups broke apart. In addition, during nighttime, none of the 15 radio-tagged birds was gregarious as was observed during daytime. Between 20 to 30 min after dusk, plovers left diurnal roosting sites and distributed themselves on the foraging mudflats all over the lagoon complex, or flew to their nighttime roosting places located close to mangroves. Some 20 to 30 min before sunrise, plovers moved to foraging sites or diurnal roosts.

Monthly variation in the use of diurnal and nocturnal feeding sites.—Wilson's Plovers showed no seasonal variation in the overall percentage of time (i.e., between 25% and 45% of day + night) spent on feeding sites ($G = 10.65$, df = 5, $P > 0.05$; Fig. 2A). However, the duration of their presence on foraging sites from November through January (Fig. 2B) was significantly longer at night than in daytime ($G = 4.20$, df = 1, $P < 0.05$; $G = 23.49$, df = 1, $P < 0.001$; and $G = 8.99$, df = 1, $P < 0.01$, for November, December, and January, respectively). The percentage of time spent at night on foraging sites increased from October to

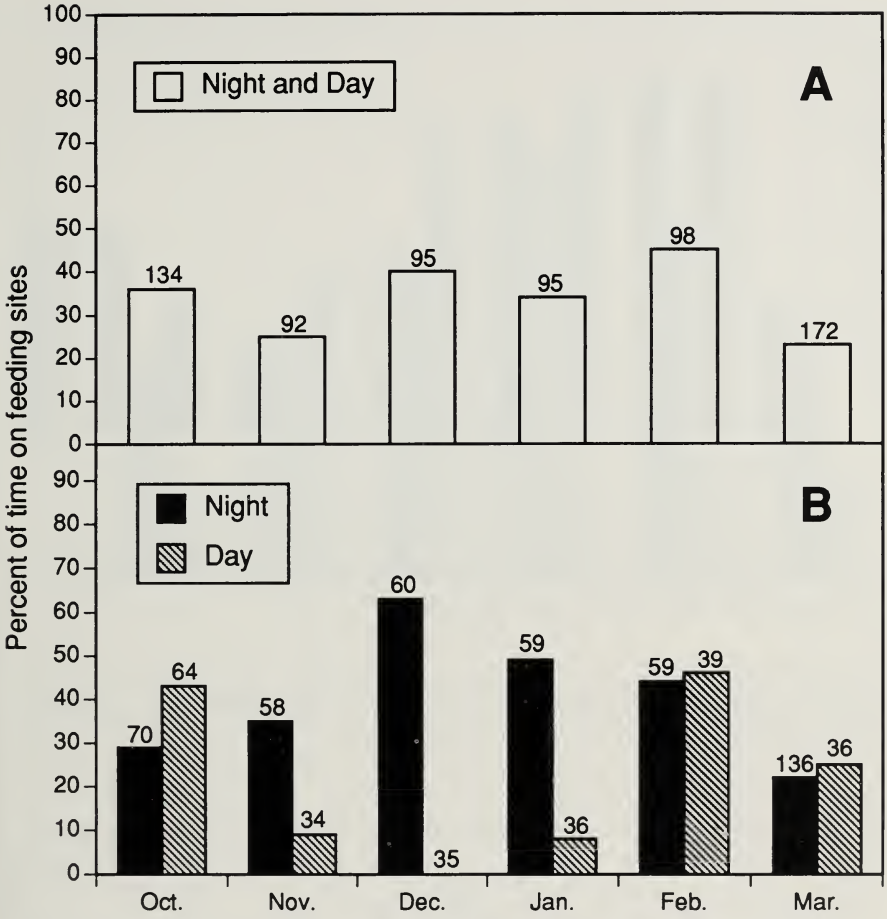

FIG. 2. Seasonal variation in the relative importance of time spent on foraging sites by Wilson's Plovers during daytime and nighttime, throughout the non-breeding season. Figures above columns represent the number of radio-tracking hours.

December and progressively decreased thereafter ($G = 5.17$, df = 1, $P < 0.05$; Fig. 2B). Plovers remained most of the day on their diurnal roosting sites during November, December, and January. In December, they foraged only at night.

Hourly variation in the use of nocturnal foraging areas.—The presence of Wilson's Plovers on their nocturnal foraging areas did not vary significantly among months ($G = 33.33$, df = 55, $P > 0.05$). However, significant hourly differences were observed ($G = 32.04$, df = 11, $P < 0.001$), with the duration of time spent on feeding areas being longer after

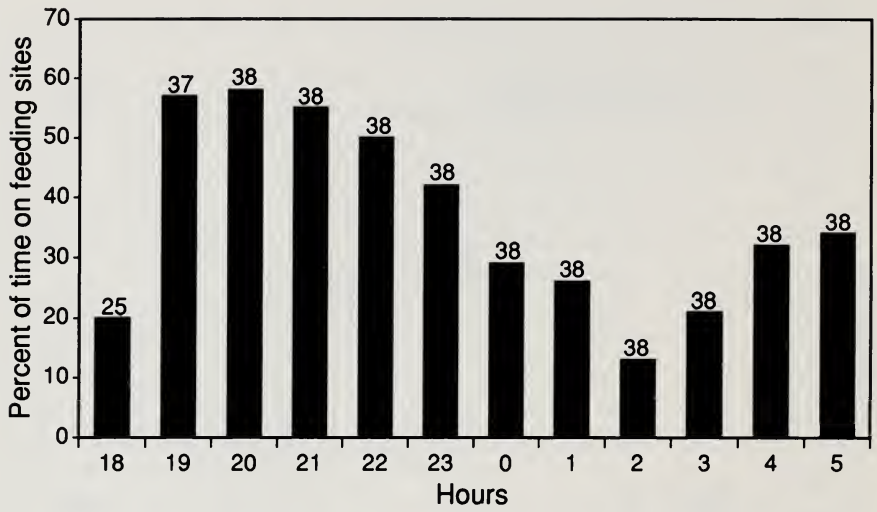

FIG. 3. Hourly variation in the relative importance of the time spent on foraging sites by Wilson's Plovers during nighttime, throughout the non-breeding season. Figures above columns represent the number of radio-tracking hours.

sunset between 19:00 and 20:00 h, progressively decreasing thereafter, and increasing slightly before sunrise (Fig. 3).

Presence on feeding areas in relation to moonlight.—Plovers used nocturnal foraging sites mainly on moonlit nights, regardless of the size of the moon disc, except in December (Fig. 4). The duration of their presence on foraging areas during moonlit nights was longer than on moonless nights during all non-breeding months combined ($t = 2.88$, df = 10, $P < 0.05$). The seasonal pattern of the use of foraging mudflats on moonlit nights tended to increase from October to January and to decrease thereafter, but monthly variation was not significant ($G = 5.13$, df = 5, $P > 0.05$). The percent of time spent on feeding habitats on moonless nights varied seasonally, but essentially because of December data ($G = 22.30$, df = 5, $P < 0.001$).

Presence on feeding areas during low tide periods.—During low tide, the presence of Wilson's Plovers on feeding habitats was generally low during daytime, except in October and February (Fig. 5). The relative importance of diurnal *versus* nocturnal presence of plovers on foraging sites did not differ significantly from one month to another between November and January ($G = 5.06$, df = 2, $P > 0.5$). Nevertheless, during all months combined, the presence of plovers on foraging mudflats was significantly longer during nighttime than during the day ($G = 73.95$, df

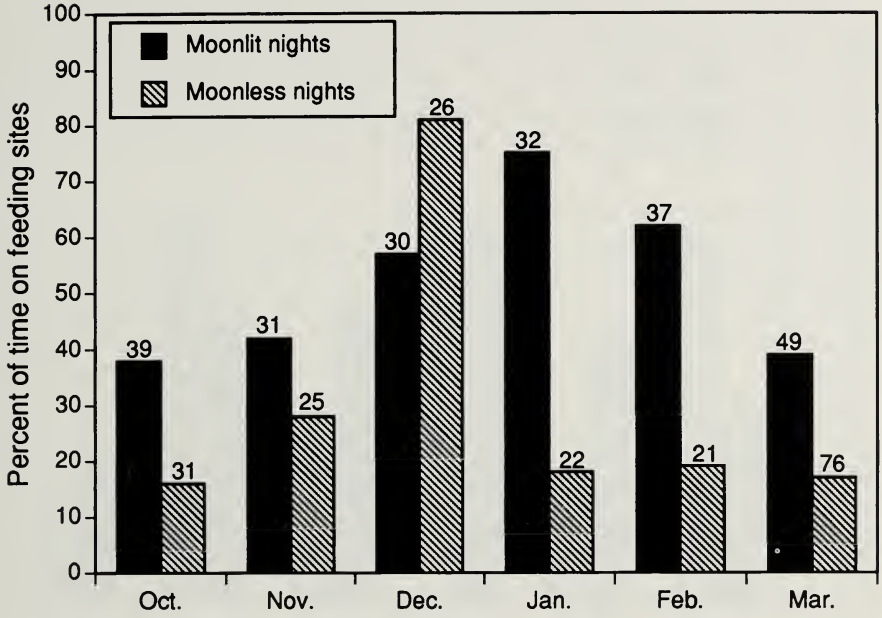

FIG. 4. Seasonal variation in the relative importance of the time spent on foraging sites by Wilson's Plovers during nighttime, as a function of the presence and absence of moonlight, during the non-breeding season. Figures above columns represent the number of radio-tracking hours.

= 3, $P < 0.001$). During the December low tides, they foraged only at night (Fig. 5).

DISCUSSION

Morrier and McNeil (1991) reported that, from November to March, daylight feeding alone was insufficient to counterbalance the energy expenditure of Wilson's Plovers at the Chacopata lagoon complex, indicating that foraging occurred primarily during nighttime. This study shows that, during the same period, the overall (i.e., day + night) time spent on foraging habitats by Wilson's Plovers did not vary seasonally. There absence on foraging sites during daylight was compensated by an increase in their presence at night. However, their diurnal presence on foraging habitats was generally low in November, December, and January but increased considerably in February. As a consequence, the overall time spent on feeding sites tended to be higher in February, but the variation was not significant. The proportion of time spent foraging is likely to vary seasonally with energetic needs. For the Wilson's Plovers of north-

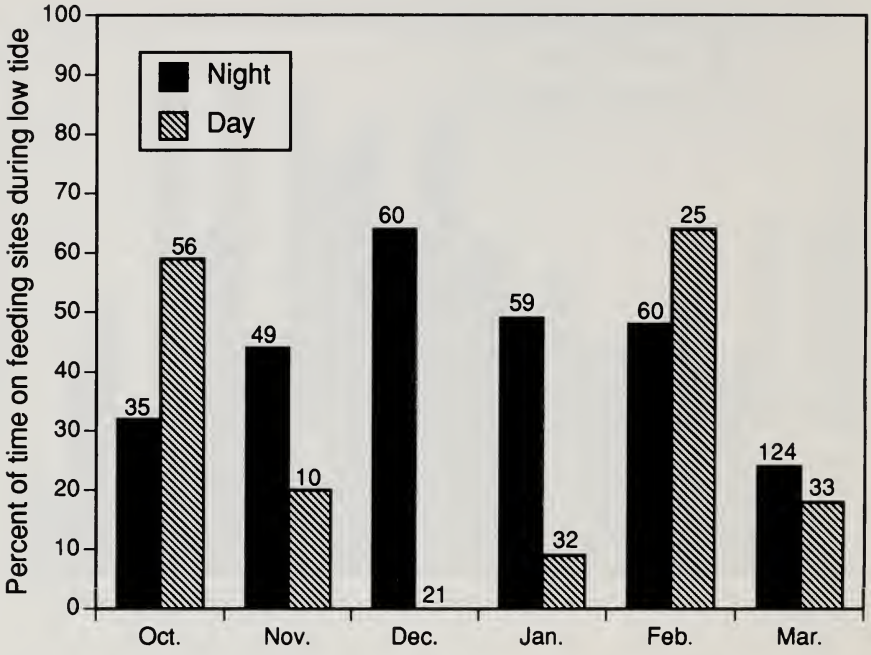

FIG. 5. Seasonal variation in the relative importance of time spent on foraging sites by Wilson's Plovers during daytime and nighttime low-tide periods, throughout the non-breeding season. Figures above columns represent the number of radio-tracking hours.

eastern Venezuela, energetic requirements are likely to be higher during the beginning of the breeding season, which starts in March–April (McNeil 1970; B. Limoges, pers. comm.; Thibault and McNeil, unpubl. data), and during the pre-alternate molt which ends in March–April (F. Mercier, pers. comm.). McNeil (1970) has shown that Wilson's Plovers of northeastern Venezuela accumulate fat reserves between mid-February and April.

The seasonal variation in the number of Wilson's Plovers on the study area during daylight suggest changes in the attachment of birds to the different roosting sites on the lagoon complex. Indeed, the plovers that roosted on sites D and E decreased progressively in number from November to January and disappeared thereafter, while the numbers on sites A, B, and C increased. It thus appears that the Bocaripo roosting sites were preferred during the period of high-water which occurs in the Chacopata lagoon complex from September to the end of January. In addition, Wilson's Plovers were present on foraging areas during nighttime throughout the study period, and from November to January, their pres-

ence at those areas was longer in duration during nighttime than during daylight. On the other hand, plovers were generally solitary during the night and gregarious during the day.

Three factors might be responsible for these differences (1) the water level, (2) the need for protection against aerial predators, and (3) the tide cycle.

The three Bocaripo sites (A, B, and C) had the following features in common: all were located on dry substrata protected from high tides. On the contrary, the wide mudflats of the lagoon complex, including the two daytime roosts (sites D and E) located north and south-east of the Chacopata lagoon, were submerged daily during the period of high waters and were wet all the time, thus not permitting the plovers to roost there.

In addition, the time when the number of Wilson's Plovers started decreasing on the roosting sites D and E and started increasing on sites A, B, and C corresponds to the time when Peregrine Falcons (*Falco peregrinus*) arrive over the Chacopata lagoon complex (Limoges 1987). Limoges (1987) also observed that many of the foraging smaller shorebirds group together more when Peregrine Falcons start chasing them over the Chacopata lagoon. Wilson's Plovers, in contrast with Semipalmated Plovers (*C. semipalmatus*), are solitary foragers (Morrier and McNeil 1991) and thus, while feeding during daylight, suffer higher individual risks of being captured by aerial predators. Being gregarious (see Vines 1971, Page and Whitacre 1975) and motionless on the Bocaripo roosts where the substrata apparently offer better daytime concealing than the wide mudflats, the Wilson's Plovers would be less exposed to predation from Peregrine Falcons or other aerial predators.

Finally, according to Strauch and Abele (1979), Wilson's Plovers forage only during low tides (Panama). On the Chacopata lagoon complex, both during nighttime and daytime, they foraged only occasionally during high tides (Robert et al. 1989, Robert and McNeil 1992, this study). The particular tide cycle of the Chacopata lagoon complex (high tides occur more frequently during daytime) could result in the need for the plovers to forage more at night and to roost during the day because the foraging habitats are submerged more frequently during daytime. Nevertheless, Wilson's Plovers never foraged during the entire low-tide periods, neither during daytime nor during nighttime.

In conclusion, as the high-tide grouping of Wilson's Plovers was observed only during the day, but never at night, and as plovers did not use the entire diurnal low-tide period for foraging, the tidal cycle cannot be invoked as the major factor responsible for their nocturnal foraging. Consequently, the main reason why Wilson's Plovers feed at night appears to be the avoidance of diurnal predators, and thus conforms to the pref-

erence hypothesis of McNeil (1991) and McNeil et al. (1992) which postulates that birds prefer to feed at night because it provides the safest feeding opportunities. Furthermore, in the Chacopata lagoon complex, Wilson's Plovers forage almost exclusively on small fiddler crabs (*Uca cumulanta,* not *U. thayeri* as mentioned by Morrier and McNeil [1991]). The Chacopata mudflats are swarming with millions of these crabs, both during day and night, and it seems quite easy for Wilson's Plovers and other shorebirds to catch them by a wait technique during the night (see Morrier and McNeil 1991). However, due to the fact that fiddler crabs, although active during the first part of the night, are principally active during daylight (Díaz D. 1993, Thibault, unpubl.), we believe that the nocturnal activity of Wilson's Plovers is not due to a daylight food shortage or higher availability of prey during the night.

Wilson's Plovers spent more time on foraging sites during the first part of the night than thereafter (Fig. 3), and on moonlit nights, although they were regularly present on feeding habitats during moonless nights as well (Fig. 4). This appears to be correlated with the activity pattern of the fiddler crabs, which are active only in this portion of the night (see above) and on moonlit nights, and practically are inactive on moonless nights (Díaz D. 1993). Nocturnal foraging, regardless of the presence or absence of moonlight, was previously reported for Wilson's Plovers by Robert et al. (1989) and Robert and McNeil (1992) and also for other shorebird species such as Grey Plovers (*Pluvialis squatarola*) (Turpie and Hockey 1993).

This study shows that the Wilson's Plover is mainly a nocturnal feeding species, and previous studies have shown that it forages visually both during moonlit and moonless nights (McNeil and Robert 1988, 1992; Robert and McNeil 1989, 1992; Robert et al. 1989). The retinal visual receptors of birds, as of all vertebrates, are rods and cones (Meyer 1977, Tansley and Erichsen 1985). Nocturnal birds have a great preponderance of rods in their retinas (Tansley and Erichsen 1985). Rojas de Azuaje et al. (1993) compared the rod/cone ratio of the Grey Plover (1.1:1.0), a visual day and night forager, with that of the Greater Yellowlegs [(*Tringa melanoleuca*) 0.7:1.0], a daylight visual feeder that switches to tactile foraging at night. However, recent results show a ratio of 1.4:1.0 for the Wilson's Plover (Rojas de Azuaje and McNeil, unpubl. data), suggesting that it is better adapted for nocturnal vision than the other species studied thus far.

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BREEDING BIOLOGY OF THE WHITE-RUMPED SHAMA ON OAHU, HAWAII

Celestino Flores Aguon[1] and Sheila Conant[2]

Abstract.—We studied the breeding biology of the White-rumped Shama (*Copsychus malabaricus*) on Oahu, Hawaii, during 1986–1987. This species is sexually dichromatic and sexually dimorphic, with males being larger. It forms monogamous pair bonds that may last two breeding seasons. The breeding season was from March through August, and territories of nesting pairs that were provided nest boxes averaged 0.09 ha in size. Only three- and four-egg clutches were observed, with four eggs being the modal clutch size. The incubation period averaged 13.6 days and the nestling period averaged 12.4 days. Both adults fed young but only the female incubated and brooded. Shamas can raise two broods in one breeding season, and reproductive success for double-brooded pairs was higher (91%) than that for single-brooded pairs (62%). *Received 4 Jan. 1993, accepted 15 Sept. 1993.*

More species of birds have been introduced to Hawaii than to any other place (Long 1981). Caum (1933) reported that 96 bird species had been introduced in Hawaii, and Bryan (1958) reported 94 introduced species. The number of accidental or intentional introductions is now estimated at 178 (Berger 1981). Little is known about the biology of most of these species, and many were introduced without prior knowledge of their ecology or their potential for impact on Hawaiian ecosystems.

The White-rumped Shama (Muscicapidae: Turdinae: *Copsychus malabaricus*), introduced to Kauai in 1931 by Alexander Isenberger, is native to South Asia, where there are four known subspecies: *Copsychus m. malabaricus* in west India, *C. m. indicus* in east India and Nepal east to northwest Burma, *C. m. leggie* in Sri Lanka, and *C. m. albiventris* in the Andaman islands south of Burma (Ali and Ripley 1973). Ali and Ripley (1973) identified the particular subspecies on Kauai and Oahu as *C. m. indicus*. In 1940, the Hui Manu Society moved White-rumped Shamas from Kauai to Oahu (Harpham 1953; Berger 1974, 1975). The exact numbers of birds involved in these introductions is not known. During the 48 years since its introduction to Oahu, the shama has spread throughout most of the island (Berger 1981).

We sought to answer several questions during the study. Does the introduced population of shamas on Oahu differ morphologically from the species in its native range? What are the basic reproductive characteristics of the shama in Hawaii (e.g., nature of the pair bond, territory size, clutch size, number of broods raised per year)? Are there any aspects of breeding

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biology that may maximize reproductive success? For example, are larger clutches or territory sizes associated with greater success, or do double-brooded pairs raise more young than single-brooded pairs?

METHODS

We studied White-rumped Shamas from January 1986 to November 1987 in Makiki Valley on Oahu; additionally two nesting pairs in Waimanalo (13 km from Makiki), Oahu, were observed in 1986. Makiki Valley lies between the ridges of Roundtop and Tantalus in Makiki State Park. The study area was about 0.4 km^2 and 121.9–304.8 m above mean sea level. Kanealole and Moleka streams dissect the area. Rainfall in the Makiki area usually does not exceed 318 cm a year, and most rainfall is recorded during November, January, and February (Taliaferro 1959). The soil is composed of volcanic ash and alluvial material, and outcrops of basalt may be found within the valley (Foote et al. 1972).

The forest is composed mainly of introduced trees, although the native koa (*Acacia koa*) may be found scattered throughout the valley. *Eucalyptus* spp., *Aleurites moluccana* (kukui), *Casuarina equisetifolia* (ironwood), *Psidium guajava* and *P. cattleianum* (guava and strawberry guava), *Citharexylum caudatum* (juniper berry or fiddlewood), *Pimenta dioica* (allspice), and *Syzygium cuminii* (java plum) are the most common species of trees. Dense thickets of hau (*Hibiscus tiliaceaus*) are found along the banks of Kanealole Stream, and impenetrable stands of *Caesalpinia dicapetala* (wait-a-bit) are found in parts of the lower valley area. Stands of ironwood trees are found mainly along a smaller ridge within the valley, and most other species of trees are scattered throughout the valley area.

We observed birds with binoculars and a spotting scope and timed their activities with a stopwatch. Prior to each breeding season, we placed nest boxes in the study area where males were known or thought to be defending territories. The boxes, made from 0.6 cm exterior plywood, were 20.3 cm high, 24.8 cm wide, and 20.3 cm deep, with a 10.2 cm diameter circular hole for an entrance. The exterior sides of the nest box were painted dark brown.

For banding and measurement, birds were captured in 36 mm mesh mist nets. Bands were placed on each tarsus, including three color bands and one U.S. Fish and Wildlife Service numbered aluminum band. To distinguish them from their siblings, newly hatched nestlings were marked on the tarsus with different colors of nail polish or permanent marker until they were banded. We made measurements with vernier calipers, a metal ruler, and Pesola scales.

Territory sizes were determined by spot mapping banded birds, usually singing males. We had divided the study area into marked 50 × 50 m grids which were transposed onto a map to allow determination of exact locations of birds. We considered twenty observation points sufficient to determine the size of each territory. To characterize patterns of male singing behavior, ten eight-minute counts were conducted monthly. The ten stations were 150 m apart, and the number, distance, and means of detection of each shama were recorded during each count (i.e., visual, call note, song).

We checked nest boxes once or twice monthly during the non-breeding season and once every other week during the breeding season to detect nesting activity. Once nest building had commenced, nests were monitored daily to determine the dates of egg laying, hatching, and hatching sequence.

We observed birds for one to three hours during days 1 (the day after the clutch was completed), 3, 6, 8, 11, 12, and 13 of incubation. Once brooding had commenced, we monitored nests for one hour every other day from day 1 to day 12 of the nestling period. To avoid excess disturbance in the nesting territories, measurements of chicks were taken

TABLE 1
MORPHOLOGICAL MEASUREMENTS OF WHITE-RUMPED SHAMAS

	Wing length (mm)	Tail length (mm)	Tarsus length (mm)	Total culmen (mm)	Nare to bill tip (mm)	Sternum (mm)	Mass (g)
Males							
Mean	90.20	134.97	28.98	16.84	11.75	22.33	31.70
SE	0.58	1.96	0.21	0.25	0.20	1.33	0.50
N	20	20	20	20	20	13	20
Females							
Mean	84.10	111.90	24.89	14.75	10.85	20.30	26.89
SE	0.88	2.12	0.33	0.27	0.14	0.58	0.35
N	17	17	17	17	17	12	16
t-test	6.0	7.99	2.85	5.74	3.61	3.01	8.34
Males[a]	86–99	108–200	25–28	17–22	—	—	30
Females[a]	84–93	102–131	25–27	18–22	—	—	30–32

[a] Values given by Ali and Ripley (1973).

on alternate days, from day 0 (hatch day) to day 10. We recorded the number and duration of feedings by each parent, and the type and length (relative to adult bill size) of the food item were recorded when possible. Observations of fledglings and juveniles were made between May 21 and July 28, 1987. We noted the date and fledging sequence of the young when they left the nest. Thereafter, we recorded the location and activities of the young and of the parents, as well as the number and type of food items fed to the fledglings.

Data were tested for normality before statistical analyses were carried out.

RESULTS AND DISCUSSION

Morphological measurements and sexual dimorphism.—We caught, banded, and measured 37 adult shamas (20 males and 17 females). Measurements taken from two adult females and two adult males in the Waimanalo Experiment Station were included in the analysis. Males were significantly larger than females in all measurements (Table 1). Shamas on Oahu were smaller or tended to be near the low end of the range of measurements given for the native Indian population (*C. m. indicus*) of the species (Ali and Ripley 1973). Berger (1981) stated that the shama in Hawaii is about 22.9 cm long, while Ali and Ripley (1973) reported the bird to be 25.0 cm long in its native range. Unfortunately, neither source provides adequate data for statistical comparison. Environmental factors (e.g., diet, climatic factors), genetic drift, and factors associated with founder effect may have influenced this possible size reduction in the Hawaiian population.

Adult shamas are both sexually dichromatic and dimorphic, males be-

TABLE 2

NUMBER OF WHITE-RUMPED SHAMAS RECORDED DURING MONTHLY COUNTS AND THE NUMBER OF ACTIVE NEST BOXES IN MAKIKI VALLEY DURING 1986–1987

Month	Mean ± SE	Range	Number of active nest boxes
November	2.7 ± 0.42	1–5	0
December	3.0 ± 0.49	1–6	0
January	6.2 ± 0.83	1–10	0
February	3.2 ± 0.73	1–7	0
March	5.1 ± 0.35	3–7	8
April	4.2 ± 0.63	2–7	21
May	5.6 ± 0.37	4–8	6
June	3.0 ± 0.37	2–5	7
July	1.4 ± 0.27	0–3	4
August	2.1 ± 0.43	0–4	0
September	3.3 ± 0.37	2–5	0
October	2.1 ± 0.43	1–5	0

ing larger. Males have a glossy black body, head and tail, and a dark chestnut chest. The female is similarly colored, but relatively drab, being grayish black to brownish. The chest is much lighter in females (Berger 1981, Pratt et al. 1987), and some females we saw had a grayish chin. Both sexes have distinct white rump and outer tail feathers.

Seasonality.—Numbers of shamas recorded per station were greater during the months of January, March, April, and May, being highest (6.2 birds/station) in January (Table 2). Most shamas were heard, not seen, so low numbers are probably due to decreased singing activity rather than an actual decrease in the number of birds present. The greatest singing activity occurred in January and decreased thereafter. In captivity there is less singing with each successive nesting attempt (J. Mejeur, pers. comm.). Nest building and egg laying were first recorded in March. Nesting activity peaked in April, when there were 21 active nests (46% of all recorded nests), and then decreased through the months of May, June, and July. The lowest level of nesting activity (other than no activity) in July corresponded to the lowest mean number of shamas recorded per station count.

Other studies have shown avian breeding seasons to coincide with or follow periods of increased rainfall (Immelmann 1971) or increases in day length (Murphy and Haukioja 1986), either of which may be followed by an increase in food availability. The Oahu shama breeding season followed a relatively consistent annual period of high rainfall (Taliaferro

1959). We suspect increased rainfall (from November to April) is correlated with increased food abundance. Shamas in India breed from March to August (Ali and Ripley 1973) during the monsoon period.

Territory and song.—Male shamas were seen within their territories throughout the year. However, it is unknown whether males defend nest sites and mates throughout the year. Feeding, nesting, and care of young occurred almost entirely within the territory. Because females are cryptic during the nonbreeding season, we could not determine whether females remained in the territory during the nonbreeding season. Captive males are aggressive towards females during the nonbreeding season (Anon. 1982), suggesting that male and female home ranges may differ at this time.

The mean territory size of nesting pairs was 0.091 ± 0.009 ha (N = 17, range = 0.011–0.154 ha). Factors that could explain the large range in territory size include available food, suitable nest sites, vegetation cover, defensive behavior of territory holders, and size of territory holder. Some of these factors are discussed later. Habitat structure may have been important, as territories were found in heterogenous habitat, e.g., in dense thickets of *Hibiscus tiliaceaus,* as well as open forest. Territories usually had some open understory, which appeared to facilitate foraging for prey on the ground.

Male and female shamas usually vocalized within their territories. Both sexes (and fledglings) made a "Tck" call, usually in response to disturbance within the territory, or just before sallying for a prey item. Males sang a complex, melodius song, but females sang short songs only during the breeding season and when in the presence of male partners. In their discussion of the White-rumped Shama, Ali and Ripley (1973) reported singing from March to May, and breeding from March to August. In our population singing did not cease during the nonbreeding season (September–February) and male shamas responded to tape playbacks of song during the breeding (March–August) and non-breeding season, indicating Oahu shamas may defend territories throughout the year. J. Mejeur (pers. comm.) observed whisper song in captive shama during non-breeding periods. If territories are held all year, increased singing may be associated with mate attraction in shamas.

We were unable to observe shama courtship behavior, and it has been reported only for shamas kept in captivity (Domin 1978:98). Our observations indicate that the White-rumped Shama is a monogamous species. The usual length of the pair bond is unknown, but we found it could be at least two years.

Nesting.—Ali and Ripley (1973) reported that only female shamas build nests. In shamas that breed in captivity, the male appears to "scout"

TABLE 3
EGG, INCUBATION, AND FLEDGLING DATA FOR WHITE-RUMPED SHAMAS IN MAKIKI VALLEY, 1986–1987

	Length (mm)	Width (mm)	Mass (g)	Incubation period (days)	Nestling period (days)	Brood size	Number of fledglings
Mean	21.80	16.02	3.12	13.61	12.31	3.13	1.71
SE	±0.20	±0.09	±0.08	±0.18	±0.24	±0.19	±0.30
Range	—	—	—	13–15	11–13	1–4	1–4
N[a]	110	110	41	18	13	23	17

[a] N = number of eggs measured or number of nests for which incubation and nestling periods and numbers of eggs hatched or young fledged were recorded.

for nest sites, but the female selects the final site and builds the nest, while the male guards unused but apparently suitable sites in the territory (J. Mejeur, pers. comm.). The nest is located within a tree cavity or hollow of bamboo and padded with rootlets and leaves. Because females appear to be easily disturbed, nest building behavior was not documented during the course of this study.

Nests in nest boxes had a large base of leaves, 3–5 cm deep, on which a depression was made where the nest cup was placed. The cup was fashioned from a layer of petioles and lined with leaves. Nesting material included dried leaves, petioles, *Casuarina equisetifolia* needles, and pieces of fern, materials typically found in the territory.

During this study 32 nests were found, and 110 eggs were measured and weighed (all eggs were weighed within 24 h of laying time). These data, as well as incubation period, nestling period, hatching success and fledging success are summarized in Table 3 for all nests and eggs recorded during the study. No significant difference in body mass or tarsal length was detected between females that laid three-egg clutches and those that laid four-egg clutches (Table 4).

Clutch size.—Three- and four-egg clutches were the only clutch sizes recorded during the two breeding seasons of this study. More nests (55% or 18 nests) had four-egg clutches than three-egg clutches (45% or 14 nests). No significant differences in length, width or egg mass, were found between the two clutch sizes (Table 4). During the 1987 breeding season, 42% or eight nesting pairs laid a second clutch. Eggs of second clutches averaged 21.63 ± 0.41 mm in length and 16.13 ± 0.20 mm in width, and 2.89 ± 0.18 g in mass. There was no significant difference in mass or dimensions between eggs in first and second clutches (Table 4). Of the eight females that laid second clutches, six laid the same number of eggs and two laid a larger or smaller clutch. According to Mejeur (pers.

TABLE 4

FEMALE SIZE, CLUTCH SIZE AND SIZE OF EGG FOR WHITE-RUMPED SHAMAS BREEDING IN MAKIKI VALLEY, 1986–1987

	Adult female			Eggs	
	Mass (g)	Tarsus (mm)	Length (mm)	Width (mm)	Mass (g)
Three eggs					
Mean	27.04	25.67	21.49	15.99	3.07
SE	±0.76	±0.42	±0.37	±0.27	±0.16
N	7	7	7	7	7
Four eggs					
Mean	27.21	24.68	22.14	16.12	3.13
SE	±1.16	±1.03	±0.85	±0.57	±0.39
N	11	12	13	13	4
t-test value[a]	0.108[b]	0.720[b]	0.560[b]	0.170[b]	0.220[b]

[a] *t*-test compared values for body and egg measurements between three-egg-clutch females and four-egg-clutch females.
[b] Not significantly different, $P > 0.05$.

comm.) shamas breeding in captivity consistently laid five-egg clutches and would usually nest five times during the season, always in the same nest site.

One egg was laid each day with incubation commencing after, but on the same day as, the last egg was laid. Eggs usually hatched synchronously within a couple of hours, and in the morning. However there were several nests in which eggs hatched asynchronously. The elapsed time between fledging of the first brood and laying of the second clutch (i.e., the first egg of the second clutch) averaged 38 ± 1.87 days (range = 11–42, N = 5). At the nest where our activities caused the first brood to fledge prematurely, the second clutch was laid about 14 days after the incident.

The sizes of eggs from 19 clutches were compared according to the sequence in which they were laid using one-way analysis of variance (ANOVA). There were no significant differences in the length, width and mass, respectively of eggs among first, second and third eggs: $F_{2} = 1.84$, df = 66; $F_{2} = 0.37$, df = 66; $F_{2} = 0.24$, df = 44 (all $P > 0.05$).

Incubation.—The average length of the incubation period for all clutches pooled was 13.61 days (Table 3). The average incubation period for second clutches was less, being 13.0 days (SE = 1.0, N = 3) but the difference was not significant ($t_{2} = 1.43$, $P > 0.05$). The average length of the incubation period was 13.9 ± 0.3 and 13.3 ± 0.21 days for three-

TABLE 5

NESTING DATA ASSOCIATED WITH THREE- AND FOUR-EGG CLUTCHES OF THE WHITE-RUMPED SHAMA IN MAKIKI VALLEY, 1986–1987

Clutch size	Incubation period	Nestling period	Number hatched	Number fledged
Three eggs				
Mean	13.90	12.30	2.60	1.90
SE	±0.30	±0.25	±0.22	±0.35
Range	13–15	11–13	1–3	0–3
N	8	8	10	9
Four eggs				
Mean	13.30	12.10	3.50	2.15
SE	±0.21	±0.31	±0.19	±0.36
Range	12–14	11–14	1–4	0–4
N	13	10	18	13
t-test values	1.71 ns[a]	0.50 ns	3.05[b]	0.48 ns

[a] Ns = not significant, $P > 0.05$.
[b] Significantly different, $P < 0.05$.

and four-egg clutches, respectively, but this difference also was not significant (Table 5). Incubation periods for shamas in Hawaii were similar to those of captive birds (Anon. 1982), but longer than the 12 days reported by Ali and Ripley (1973). The difference in incubation period may be real, or the result of differences in measurement of the incubation period. Captive shamas incubated their five-egg clutches 14 to 14.5 days (J. Mejeur, pers. comm.), and hatching took place over a two-day period.

Although Berger (1981) suggested that both adults incubate, we found only females incubating. In addition, none of the ten adult males that were caught during the breeding season had a brood patch. Males flew to the nest box during the incubation period (29 instances noted), but not all males exhibited this behavior. Most of these visits occurred during the middle of the incubation period. Typically, the male would fly to the nest box and perch on the rim, look inside and then fly away. On one occasion the male entered the nest box and pecked at the nesting material before leaving. We never observed male shamas bringing food to the nest during the incubation period; however, J. Mejeur (pers. comm.) occasionally observed this behavior in captive-breeding males.

Attentive periods (the time that a bird spent on eggs) gradually increased up to the eighth day of incubation and then decreased lightly afterwards. Mean attentiveness during the incubation period ranged from

13.90 ± 4.75 minutes on day one of incubation to 30.83 ± 4.20 min on day six. One-way ANOVA indicated that differences in the length of attentive periods on different days of the incubation period were significantly different from one another: $F_s = 2.37$, df = 89, $P < 0.05$. Although sample sizes were small, we did find that attentive periods for females with four-egg clutches tended to be longer, but not significantly so, than those with three-egg clutches. In a study of the House Wren (*Troglodytes aedon*), Baldwin and Kendeigh (1927) found that periods of attentiveness and inattentiveness were quite regular in duration; however, during the last three days of incubation, attentiveness increased but the duration of inattentiveness remained the same. Similarly, Domin (1978) found attentiveness in captive shamas to increase late in the incubation period.

Eggs usually hatched during early morning, though some hatched after noon. The average number of eggs hatched from first clutches was 3.17 ± 0.20 (N = 23). Four-egg clutches hatched significantly more young (3.5) than three-egg clutches, which averaged 2.6 young (Table 5). Second clutches on average hatched 3.40 ± 0.24 young (N = 5). Thus females that laid a second clutch had about 30% greater reproducive success (measured as number of young hatched) than females laying a single clutch. Because results were based on a single breeding season, we could not determine the effects of female age on reproductive success. Sample size was too small (N = 4, one clutch did not hatch) to determine if production of second broods was correlated with territory size, male size, or other factors.

Predation was not a major factor in egg losses during the incubation period. Only one nest at the egg stage (2.56% of the total) was preyed upon, possibly by rats (*Rattus* spp.). Other potential predators on eggs are mongooses (*Herpestes auropunctatus*), which are common in Makiki Valley (pers. obs.), and feral cats (*Felis catus*).

Nestling period and parental care.—Nestlings hatched blind and naked but responded to tapping on the nest box by gaping and exposing a bright yellow target in their mouths. At two days of age, the outlines of wing feather tracts were visible, and pin feathers erupted through the skin at four days. At six days, the eyes began to open and young were able to make soft "pipping" sounds. At about eight days old, primary and secondary feathers broke through the feather sheaths and all other tracts were clearly visible. By age ten days, feathers in all tracts had broken through their sheaths, and the young had begun preening themselves.

The nestling period of first broods averaged 12.31 ± 0.24 days (N = 13), and for second broods averaged 11.80 ± 0.37 days (N = 5) but these were not significantly different ($t_s = 1.15$, df = 16, $P > 0.05$). There were no significant differences between three- and four-egg clutch-

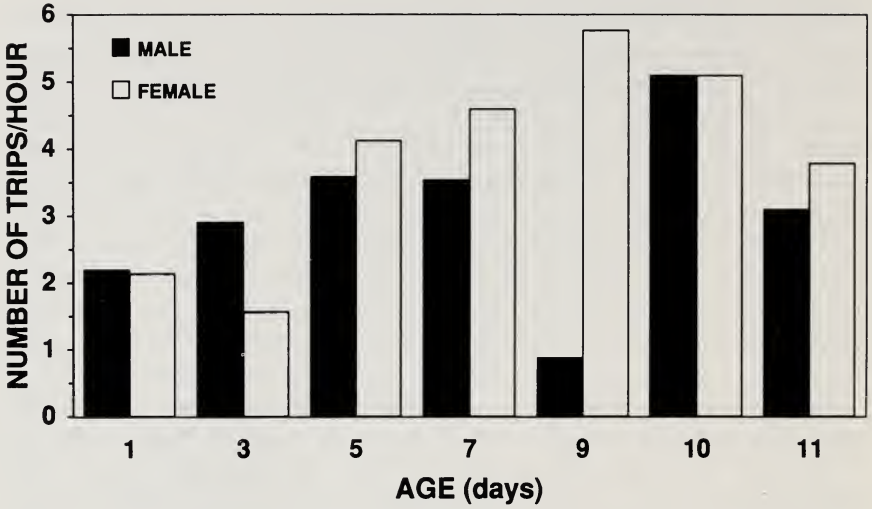

FIG. 1. Feeding trips made by adult White-rumped Shamas during the nestling period.

es in the length of the nestling period (Table 5). In captivity the nestling period is about 14 days (J. Mejeur, pers. comm.).

Observations of brooding behavior were made when nestlings were one to nine days old. Although both males and females removed fecal sacs from the nest, we observed only females brooding. Brooding ceased by the ninth day. Brooding averaged 11.77 ± 5.61 min per session at day one, then increased, averaging 17.14 ± 2.58 min per session on day three. Brooding decreased in subsequent days to 2.93 ± 1.23 and 1.13 ± 0.60 min per session on the fifth and seventh day, respectively.

Males fed nestlings more often than females (although not significantly more) when nestlings were one to three days old (Fig. 1). While females brooded, males delivered food to the female, who then fed the young, but only during the first five days of the nestling period. However, females tended to feed nestlings more often after day three. When young were ten days old, both parents fed young at approximately equal frequencies.

Two cases of cooperative breeding behavior were observed. At each of two nests, two different males were observed feeding young that belonged to a single female. At one nest when the single nestling hatched from a clutch of four eggs was nine days old both banded and unbanded males were seen feeding it. The female had been banded the previous day, so she could not have been confused with the second male. Both males were seen again feeding the nestling when it was 10 and 12 days old. There was no apparent aggression between the two males. A similar

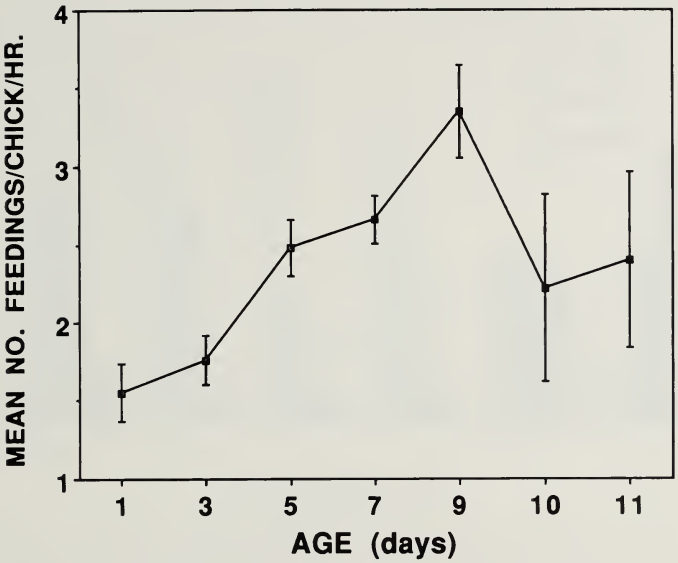

FIG. 2. Feeding rates of White-rumped Shama chicks. Vertical lines indicate ± 1 SE.

situation occurred at a nearby nest, but this time we observed aggressive behavior by the territorial male towards the intruder male. At this nest both parents were banded and the intruder male was not. Despite repeated attacks by the banded male, the unbanded male made repeated attempts to feed the young (he had food in his bill) and fed the young three times.

Feeding frequency increased as chicks got older until they were ten days old (Fig. 2). The subsequent decrease in feeding frequency may be associated with an actual reduction in nestling growth rate, as well as increased search time required to find food. The latter idea may be supported by the shift in food size during the mid- to late-nestling period (Fig. 3).

When young were newly hatched, parents fed mostly smaller food items. When young were five to nine days old, parents fed mostly larger food items. At five days of age, young were given larger foods (mainly earthworms) 55% of the time. At seven days of age young were given large foods 70% of the time. This amount decreased to 54% at nine days; then there was a shift to medium sized items. Because territories are quite small large food items may be substantially depleted by the time nestlings fledge. The types of food items fed to the young included adult insects (53%), earthworms (36%), unidentified adult arthropods (<8%), arthropod larvae or pupae (<3%), and skinks (<1%).

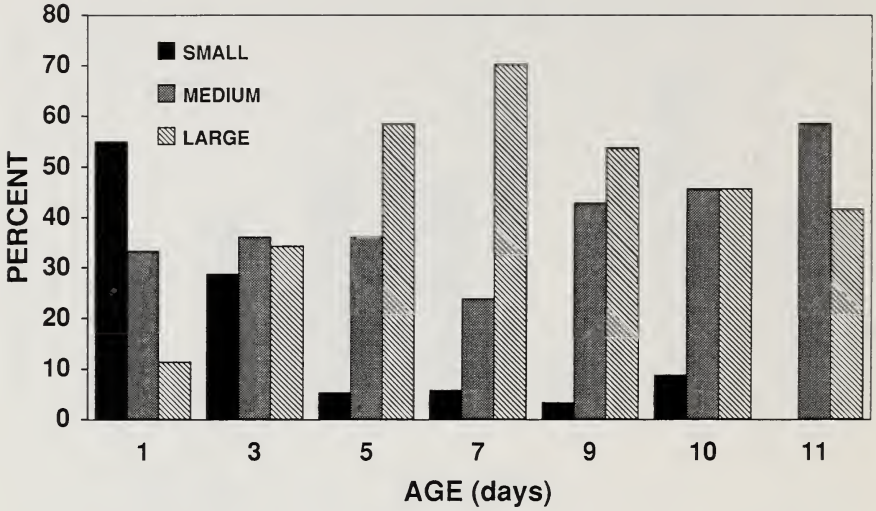

FIG. 3. Food size categories and age of White-rumped Shama nestlings. Small, medium, and large food items were smaller, approximately equal and larger, respectively, than the adult bird's bill (N = 209).

As Ali and Ripley (1973) reported for Indian shamas, both sexes on Oahu shared in feeding the young. In captive shamas, both sexes feed the young, but the female usually consumes or removes the fecal sacs (Anon. 1982). However, in this study both sexes were found to remove fecal sacs. Males removed fecal sacs approximately as often (53.3%, N = 107 observations) as females (46.7%). The parents swallowed the fecal sacs when the nestlings were young, or disposed of them away from the nest.

Nestling growth and survival.—Nestlings were measured on alternate days from the day of hatching to the tenth day (Figs. 4 and 5). The initial average mass of nestlings was 2.67 ± 0.09 g (N = 61). The average mass gain per day was 2.52 g until the eighth day when the rate decreased to 2.12 g per day. Average nestling mass gain between the eighth and tenth day was 0.64 g, or approximately 0.3 g per day. Mean nestling mass at ten days old was 22.32 ± 0.40 g (N = 53), 70.4% or 83% the weight of the mean weights of adult males or females, respectively.

The rapid mass gain of nestlings may be compared to the feeding rates of parents. The mass curve (Fig. 5) becomes asymptotic at the eighth day and corresponds to the lower feeding rates by the parents in subsequent days. The young may not require as much food during the few days before fledging because of a real reduction in growth rate. A prolonged nestling period, after asymptotic mass, is common among cavity nesters (von

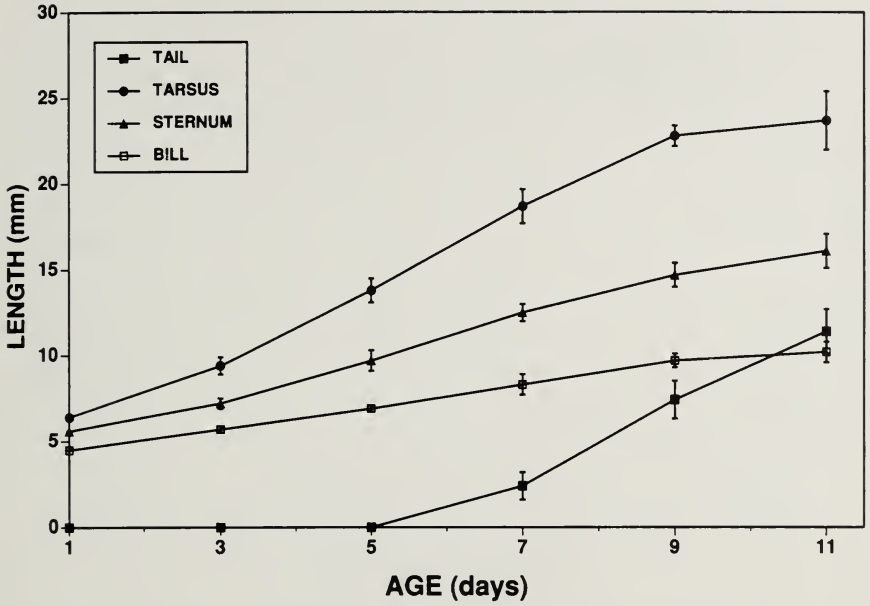

FIG. 4. Growth of tail, tarsus, sternum, and bill of White-rumped Shama nestlings of all broods combined. Vertical lines indicate ± 1 SE.

Haartman 1975). Freed (1988) found that tropical House Wrens (*Troglodytes aedon*) may remain in the nest at asymptotic mass for up to a week. Perhaps the feather development and maturation of both morphology and physiological processes known to occur at this time require less food (see Ricklefs 1984 for review).

We plotted nestling growth curves of tail, tarsus, sternum and bill (Fig. 4). Sternum length of newly hatched nestlings averaged 5.55 ± 0.01 mm (N = 61) and increased continually to 16.02 ± 0.16 (N = 42) at ten days of age. This length was about 72% or 79% of that of adult males or females, respectively. Tarsus length of newly hatched nestlings averaged 6.36 ± 0.13 mm (N = 61) and was 23.57 ± 0.82 mm (N = 42) at day ten. Tarsi of ten-day-old nestlings were about 91% or 95% the length of tarsi of adult males or females, respectively. Newly hatched nestlings' total bill length averaged 4.45 ± 0.05 (N = 61). At ten days of age nestling bill length averaged 10.27 ± 0.27 mm (N = 42), and measured 61% or 73% the size of adult male or female shamas, respectively.

Development of wing and tail feathers is shown in Figs. 4 and 5, respectively. The wing chord of newly hatched nestlings averaged 6.66 ± 0.09 mm (N = 61). This value actually is the length of the alula

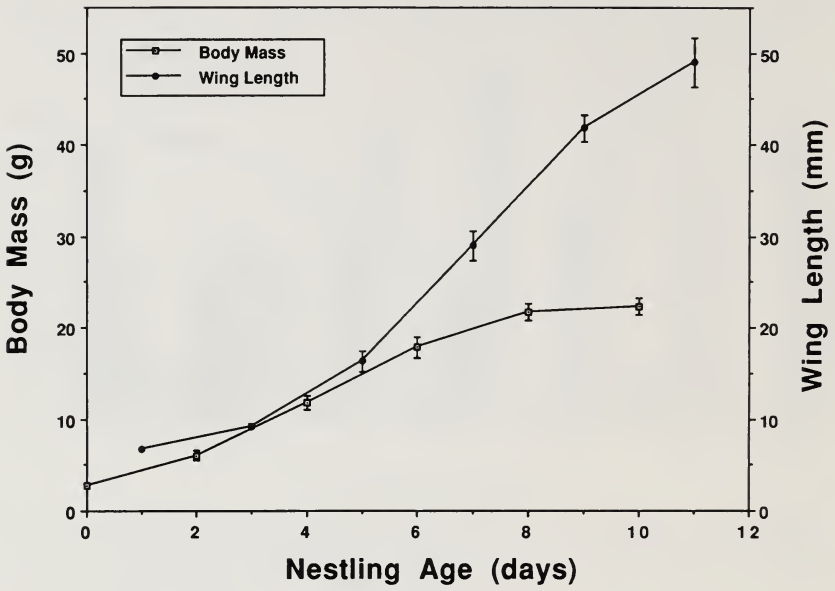

FIG. 5. Growth of wing and mass of White-rumped Shama nestlings of all broods combined. Vertical lines indicate ± 1 SE.

because nestlings are born naked. The wing chord length of ten-day-old nestlings averaged 48.78 ± 1.79 mm (N = 42), 54% or 58% of the wing length of adult male or female shamas, respectively. The tails of nestlings showed the most delayed development compared to the other parts measured. Tail feathers did not erupt from the feather tract until after the fifth day, and on the sixth day averaged 1.82 ± 0.12 mm (N = 37). At ten days old, nestling tail length averaged 11.25 ± 0.52 mm (N = 26), and 8% or 13% the length of the tail of adult male or female shamas, respectively.

Nestling survival from hatching until ten days old was 68.8%. Two nests (10.5%, N = 19 nests) lost all young. One nest with a brood of three was depredated after the eleventh day of the nestling period, and another nest with a brood of four lost all nestlings between the fourth and sixth day of the nestling period. Predation does not appear to be a major factor in nestling mortality. Young fledged when about 12 days of age. Fledging success of first broods aveaged 1.71 ± 0.30 young (N = 17). Second broods on average fledged 2.8 ± 0.45 young (N = 5) or 1.09 more young than the first broods, but this was not a significant difference.

Fledging.—Banded fledglings were observed within their natal territories up to 54 days after fledging. The last day that parents were observed to feed young was the 26th day after fledging. However, fledglings may remain on the territory for a longer period without care from their parents. On 11 June 1987, 26 days after the young of one nest had fledged the probable father of the fledgling came within two meters of a banded fledgling as both foraged on the ground. The fledgling did not beg from the male nor did the male attempt to feed the young bird. Four days earlier begging calls had been heard within the territory.

In his captive shamas, J. Mejeur (pers. comm.) observed that females were more likely to feed newly fledged chicks than those of the previously-fledged brood. He found that males, on the other hand, did most of the feeding of fledglings if the female was incubating a new clutch; he would continue to feed older fledglings even after the next brood fledged. Mejeur found that the fledgling period usually lasted about a month.

If newly mature shamas are unable to become part of the breeding population or to secure a territory, they may form flocks outside of defended breeding territories (this was never observed) or live solitarily and spend some time in other breeders' territories (Smith 1978). Because nesting sites may be limiting for this cavity-nester (van Balen et al. 1982, von Haartman 1957), these behaviors seem likely.

Reproductive success.—Although competition among hole-nesters for nesting sites may be intense, van Balen et al. (1982) suggested that their nesting attempts are usually more successful than those made by open-cupped or roofed nesters (about 10 to 20%; see Ricklefs 1969). Fledging success of all shama first broods was 65.7 ± 9.6% (N = 17). This percentage is comparable with fledging success of hole-nesters in North America (66.0%, Nice 1957, Ricklefs 1969), and greater than the 43.6% success reported for Costa Rica hole-nesting species (Skutch 1966).

Shamas that laid two clutches during the breeding season had greater fledging success than those that laid a single clutch, and parents that raised a second brood were able to fledge more young in relation to the number of eggs that hatched. The proportion of hatched young that fledged was larger in second broods (Mean = 0.832 ± 0.71, N = 5) than in first broods (Mean = 0.657 ± 0.097, N = 17) but not significantly so (Table 6). Survival rate of ten-day-old nestlings of all first broods was 77.7% but fledging rate was only 63.8%; whereas, the same age nestlings of second broods had a survival rate of 94.1% and a fledging rate of 82%. However, ten-day-old nestlings from second broods were significantly lighter than the average of those in first broods (t_s = 1.96, df = 41, $P >$ 0.05). This suggests that there may be less food available within the territories of shamas raising second broods.

TABLE 6

REPRODUCTIVE SUCCESS OF SINGLE- AND DOUBLE-BROODED PAIRS OF WHITE-RUMPED SHAMAS IN MAKIKI VALLEY IN 1986–1987

	Mean % of eggs hatched	Mean % of eggs surviving to fledgling	Mean % of hatchlings fledged
All first broods	0.855 (23)[a]	0.495 (17)	0.657 (17)
Single brood pairs[b]	0.856 (18)	0.474 (13)	0.615 (13)
Double brood pairs	0.817 (5)	0.715 (5)	0.875 (5)
All second broods	0.950 (5)	0.790 (5)	0.832 (5)
Both broods combined[c]	0.850 (4)	0.770 (4)	0.906 (4)

[a] Sample sizes are in parentheses.
[b] These values represent total reproductive success for single-brooded pairs.
[c] These values represent total reproductive success for double-brooded pairs.

Shamas that raised two broods had a fledging success of 87.5% for the first brood. Total fledging success of pairs raising two broods (the mean number of young fledged from both broods divided by the mean number of young hatched) averaged 90.6 ± 0.9% (N = 4). However, this was not significantly different from the success rate of all first broods, possibly because sample sizes were small. The proportion of young fledged from second broods may be a reflection of parental age, parental physical condition, territory size and quality, or food abundance.

Many factors that promote higher reproductive success in birds have been documented. Perrins and McCleery (1985) studied reproductive success in Great Tits (*Parus major*) and found that age played an important role in terms of laying date, clutch size, number fledged, and number of offspring surviving to breed. They found that pairs with two older members had a higher reproductive success compared to pairs which had a first year member (male or female). Pairs with young males tended to lay later in the season, have smaller clutches, and have fewer young and survivors than pairs with older males. Pairs with young females tended to lay later and have smaller clutches than those with older females. In a study of the European Robin (*Erithacus rubecula*), Harper (1985) found that males with large territories were more likely to pair and tended to pair earlier than those defending small territories. In that study, female breeding success, based on the number of independent young, was positively correlated with the size of the territory. Finally, Perrins (1965) found that the incidence of second broods in Great Tits appeared to be related to food supply.

Reproductive success did not differ between shama pairs laying three- and four-egg clutches. Territory size of three- and four-egg pairs was not

significantly different. Food abundance within the territories at the time of egg laying or during the nesting period might explain differences, but we have no data on this factor. Shama pairs raising two broods tended to be early nesters, laying the first clutch in April, whereas eggs of single-brooded pairs were laid between the beginning of May and mid-June.

Number of clutches rather than clutch size per se appears to be important in White-rumped Shama reproductive success. Our study suggests that individuals with two broods realize greater reproductive success per breeding season. An assumption underlying this conclusion is that the fledged progeny of pairs raising two broods have equal (or greater) survival in comparison to young of parents raising one brood. Though double-brooded pairs appear to have greater fitness in a single season, they must increase reproductive effort and may thereby reduce their future reproductive potential (Williams 1966). However, lifetime reproductive success of single- and double-brooded pairs must be determined before any definitive conclusion can be made.

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RELATIONSHIP OF BODY SIZE OF MALE SHARP-TAILED GROUSE TO LOCATION OF INDIVIDUAL TERRITORIES ON LEKS

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Abstract.—We examined size differences in four morphometric characters of 52 male Sharp-tailed Grouse (*Tympanuchus phasianellus*) occupying central and peripheral territories on six leks near Fort Albany in northeastern Ontario. Univariate and multivariate analyses showed that central males, which were all adults, were significantly larger than peripheral individuals, some of which were juveniles. Central males were disproportionately heavier for their body size than peripheral males. Differences in body condition may permit central males to attend the lek for longer periods of time and display more than their peripheral neighbors. Body size as well as body condition may be important in male-male interactions involving territory acquisition and maintenance on the lek. *Received 18 May 1993, accepted 21 Sept. 1993.*

Sharp-tailed Grouse (*Tympanuchus phasianellus*) exhibit lekking behavior in which males establish territories in aggregates and display within sight of each other on open, relatively flat habitat (Hjorth 1970, Hoglund 1989). These territories are maintained by males on an infrequent basis for most of the year but are visited on a daily basis during the breeding season (Moyles 1977, Kermott 1982). Females visit the mating arena for the sole purpose of mating (Bradbury 1977, 1985); they show a marked preference for males occupying centrally-located territories on the lek (Lumsden 1965, Evans 1969, Hjorth 1970).

Individual males of the lek get central territories sequentially; juvenile males first establish territories on the lek periphery and move centripetally as vacancies become available (Evans 1969, Rippen and Boag 1974, Kermott 1982). Thus, older males occupy central territories and more peripheral territories are occupied by younger individuals (Rippen and Boag 1974). Although chance events (e.g., death) can have a major role in gaining a central territory, occupancy of a preferred central territory can be maintained only by daily visits to the lek to display and defend territorial boundaries (Kruijt et al. 1972, Wiley 1973, DeVos 1983). It has been hypothesized that male-male interactions, such as in territorial defense, competitive ability of an individual can be enhanced through an increase in body size (Clutton-Brock et al. 1977). Here we examine morphological variation of males on leks of Sharp-tailed

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Grouse and relate male age and body size to territorial position in the lek.

STUDY AREA AND METHODS

Study sites were in areas of muskeg near Fort Albany, Ontario (52°15′N, 81°35′W), on the west shore of James Bay (Hanson 1953). One of us (L.J.S.T.) accompanied several native North Americans on their spring hunt for Sharp-tailed Grouse in the above area and examined birds killed on these hunts.

A total of 52 males was examined from six separate leks during the 1990–1992 breeding seasons. Adults were distinguished from juveniles on the basis of appearance and wear of primary feathers (Ammann 1944). At the time of collection, L.J.S.T. scored males as those possessing either central or peripheral territories. Central differed from peripheral territories by having neighboring territories on all sides (Hogan-Warburg 1966, Kruijt and Hogan 1967).

Four morphological variables were measured on each bird as follows: bill length, measured from the anterior edge of the nostril to the bill tip; wing length, the flattened wing length from the bend in the wing to the tip of the longest primary; tarsometatarsus length, the bone measurement from the tip of the intercondylar prominence to trochlea for digit III; body mass, fresh weight taken immediately following collection of specimens. Linear measurements were made with vernier calipers to the nearest 0.05 mm except wing length which was taken with a ruler to the nearest 1.0 mm. Body mass was measured to 1.0 g with either a spring scale or triple-beam balance.

The data were analyzed by multivariate and univariate procedures (SAS Inst. 1982). Variables were transformed to natural logarithms and samples for central and peripheral males were normally distributed at the $\alpha = 0.01$ level (Shapiro-Wilk's test, Shapiro and Wilk 1965). Variation in character means between central and peripheral males was assessed multivariately by single-classification multivariate analysis of variance (MANOVA) and univariately by single-classification analysis of variance (ANOVA). The structure of covariation among the characters was determined using principal component (PC) analysis. The first three PCs and associated eigenvalues were extracted from a total correlation matrix of the four characters. Bootstrapping (Efron 1982) was used to avoid making a subjective interpretation of the "meaning" of the principal components. Data were randomly sampled 1000 times with replacement and 95% confidence limits determined for estimates of PC coefficients and eigenvalues using the percentile method (Efron 1981). PC scores were calculated for each individual on the first component and compared between central and peripheral birds by ANOVA. The relationship between body mass and body size among individuals was assessed by linear regression analysis.

RESULTS

Age, morphological variation, and territorial position.—Of 52 birds examined, 40 (76.9%) were adults, while 12 (23.1%) were juveniles. Age of males was highly (χ^2 adjusted for continuity = 13.1, $P < 0.0001$) related to position of territory (i.e., peripheral or central). Only adult males (N = 26) occupied central territories. Fourteen (46.2%) adult males held peripheral territories, with the remaining 12 used by juveniles.

MANOVA of the four measured characters indicated a significant dif-

TABLE 1

MORPHOMETRIC CHARACTERS, AND ANOVA BETWEEN MALES OCCUPYING PERIPHERAL AND CENTRAL TERRITORIES OF SHARP-TAILED GROUSE

Character	Peripheral males (N = 26) $\bar{x} \pm$ SD	Central males (N = 26) $\bar{x} \pm$ SD	F^a
Body mass, g	847.27 ± 33.41	912.14 ± 29.90	54.62***
Tarsometatarsus length, mm	45.80 ± 0.89	46.89 ± 0.77	22.18***
Wing length, mm	215.15 ± 4.03	219.04 ± 6.30	7.01*
Bill length, mm	12.50 ± 0.35	13.02 ± 0.45	21.50***

[a] Significance of F: * = $P < 0.05$; *** = $P < 0.001$.

ference (F approximation of Wilk's lambda = 19.51, df = 4 and 47, $P < 0.0001$) between males on peripheral and central territories. Similarly, a significant difference (F approximation of Wilk's lambda = 10.54, df = 4 and 35, $P < 0.0001$) between adults on peripheral and central territories was noted. Further, among peripheral individuals, a significant difference (F approximation of Wilk's lambda = 6.45, df = 4 and 21, $P = 0.0015$) between adults and juveniles was shown. ANOVA of each character showed that males on central territories were significantly heavier and had larger tarsometatarsus, wing, and bill than males on peripheral territories (Table 1). Among adults, significant differences ($P < 0.037$) between central and peripheral males were found for body mass, tarsometatarsus length, and bill length but not for wing length ($P = 0.1339$). For peripheral birds, adults exceeded juveniles significantly only in mass (Table 2).

Character covariation.—Boot-strapped coefficients of the first three principal components (PC), their associated eigenvalues, and estimated 95% confidence intervals varied (Table 3). The PCs combined accounted

TABLE 2

MORPHOMETRIC CHARACTERS, AND ANOVA BETWEEN JUVENILES AND ADULT MALES OCCUPYING PERIPHERAL TERRITORIES OF SHARP-TAILED GROUSE

Character	Juvenile males (N = 12) $\bar{x} \pm$ SD	Adult males (N = 14) $\bar{x} \pm$ SD	F^a
Body mass, g	823.13 ± 26.59	867.97 ± 23.42	20.89***
Tarsometatarsus length, mm	45.46 ± 0.79	46.09 ± 0.89	3.63
Wing length, mm	213.92 ± 4.29	216.21 ± 3.60	2.25
Bill length, mm	12.40 ± 0.31	12.59 ± 0.37	1.85

[a] Significance of F: *** = $P < 0.001$.

TABLE 3

BOOTSTRAPPED PRINCIPAL COMPONENTS AND ASSOCIATED EIGENVALUES (λ) OF MORPHOMETRIC CHARACTERS OF SHARP-TAILED GROUSE

Character	PC1		PC2		PC3	
	Coeff.	95% CI	Coeff.	95% CI	Coeff.	95% CI
Body mass	0.849	0.751, 0.917	−0.191	−0.498, 0.160	−0.092	−0.420, 0.394
Tarsometatarsus length	0.816	0.651, 0.908	−0.154	−0.527, 0.357	−0.098	−0.597, 0.632
Wing length	0.449	−0.023, 0.752	0.685	−0.603, 0.988	0.180	−0.573, 0.717
Bill length	0.689	0.416, 0.839	0.058	−0.622, 0.849	0.138	−0.680, 0.755
λ	2.122	1.771, 2.505	0.924	0.725, 1.098	0.637	0.439, 0.839

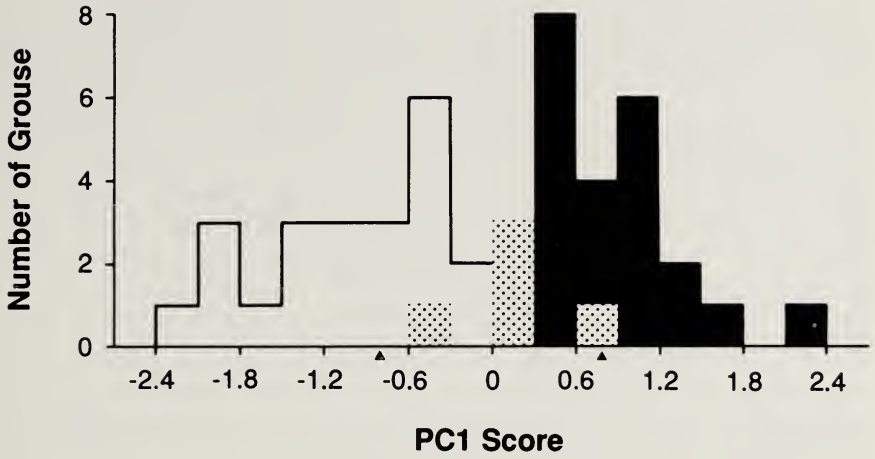

FIG. 1. Frequency distribution of individual scores on the first principal component (PC1) based on four morphometric characters of Sharp-tailed Grouse on peripheral (open histogram) or central (solid histogram) territories in six leks. Overlap in histograms is shown by the stippled areas. Triangles indicate multivariate means for each sample.

for 92.1% of the total variation. Confidence intervals that do not include zero identified coefficients significant at the $\alpha = 0.05$ level. Significant coefficients were identified only on PC1, which explained variation in body mass and lengths of tarsometatarsus and bill. Frequency distributions of individual scores along PC1 illustrate the distinctiveness between peripheral and central males in terms of multivariate size (Fig. 1). Large central males had correspondingly high values on PC1 relative to peripheral males. ANOVA showed a significant difference ($F = 74.40$, $P < 0.001$) in PC1 scores between the two groups.

Relationship between body mass and body size.—Length of tarsometatarsus was used as a measure of body size in comparing variation in body mass of males occupying peripheral vs central territories. Linear regression analysis showed that 39.1% ($r = 0.62$, $P < 0.0001$) of the variation in body mass was attributable to variation in tarsometatarsus length (Fig. 2). Among central males, 73.1% had values of body mass that exceeded those predicted by the regression equation, while 69.2% of peripheral males had values of body mass lower than predicted. ANOVA of residual variation between peripheral and central males was significant ($F = 15.10$, $P = 0.0003$). Thus, central males were disproportionately heavy for their body size when compared to their peripheral counterparts.

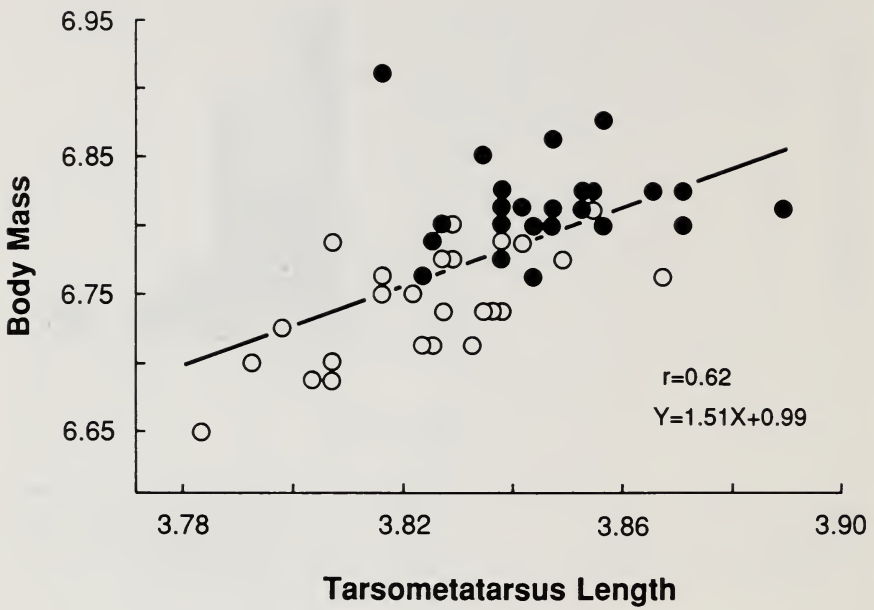

FIG. 2. Relationship between the natural log of body mass and tarsometatarsus length of 52 Sharp-tailed Grouse occupying peripheral (○) and central (●) territories in six leks.

DISCUSSION

Only adult Sharp-tailed Grouse males occupied central territories while peripheral territories contained approximately equal numbers of juveniles and adults. This supports previous findings that most males gradually move centripetally on the lek filling vacancies that occur naturally (Moyles 1977, Kermott 1982). Central territories are only rarely acquired by direct aggressive behavior; however, survivorship, site fidelity, and aggressiveness are of importance in acquiring preferred territories (Moyles 1977, Kermott 1982).

In male Sharp-tailed Grouse, large body size is of known importance when territories initially are established on the periphery of the lek (Moyles 1977, Gratson 1989). Furthermore, Nitchuk (1969) found that males occupying the preferred central territories were larger than individuals at the periphery; however, differences in mean body mass were not significant. In the present study, coefficients on PC1 all had positive, mainly large values with PC1 being interpreted as a multivariate measure of overall size (Jolicoeur and Mosimann 1960, Blackith and Reyment 1971). The observation that central males are larger than peripheral individuals is consistent with the competitive hypothesis (Clutton-Brock et

al. 1977). Furthermore, all differences were not attributable to age, because adults occupying peripheral territories were significantly smaller compared to their central counterparts.

Although absolute body size may be important in male-male combat and obtaining territories (Emlen 1976), health of an individual is also of importance in maintaining a preferred territory because daily attendance at the lek by males is required to maintain territorial boundaries (Kermott 1982, DeVos 1983). Relative body mass as related to body size is a good indicator of general health (Vehrencamp et al. 1989). Adult males in peripheral territories, although not significantly different from juveniles in linear measures of body size, were significantly larger in body mass and therefore may have physiological advantages over juveniles. Increased mass may enhance length of fasting in seasonal environments. On cold days when thermoregulatory demands increase (Gibson and Bradbury 1985), large males may be able to attend the lek for longer periods and display more than smaller peripheral males. Also, endogenous reserves may be of importance during short periods of high energy demands (Hupp and Braun 1989), for example, during peaks of attendance of females at the lek, when male display rates are greatest (Kermott 1982).

Occupancy of a central territory does not by itself guarantee mating success, as some centrally located males on a lek do not mate (Hartzler 1972). It appears that occupying a central territory allows an individual to be part of a subset of males at the lek that are preferentially examined by females with actual mating preference depending on some other variable. In Sage Grouse (*Centrocercus urophasianus*), display rates among territorial males have been shown to be positively correlated with mating success (e.g., Hartzler 1972). Furthermore, males that display most actively on a lek lose less mass per day compared to males that display less vigorously (Vehrencamp et al. 1989). Condition or the ability to maintain condition may be the actual variable of importance in female mating preference at the lek.

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METABOLIC RATE OF AMERICAN WOODCOCK

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Abstract.—We measured metabolic rate of captive-reared American Woodcock (*Scolopax minor*) by indirect calorimetry. Basal metabolic rate (BMR) averaged 1.22 ± 0.18 ml O_2 $g^{-1}h^{-1}$ (N = 5). Lower critical temperature was 22°C. Below thermoneutrality, the relationship between metabolic rate (VO_2) and ambient temperature (T_a) was best described by the equation: $VO_2 = 2.047 - 0.0375(T_a)$, ($r^2 = 0.62$, N = 29). Although BMR for American Woodcock was greater than that predicted by some generalized equations for non-passerines, it did not follow the elevated pattern for shorebirds predicted by the equation of Kersten and Piersma (1987). Lower BMR in American Woodcock may result from lower annual peaks of energy use compared to other shorebirds. *Received 29 Jan. 1993, accepted 15 Sept. 1993.*

Laboratory measurements of metabolic rate have been reported for few shorebirds. In those shorebirds that have been studied, metabolic rates were consistently above those predicted by published allometric equations for non-passerines (Castro 1987, Kersten and Piersma 1987, Mathiu et al. 1989), prompting Kersten and Piersma (1987) to develop a separate equation specific to shorebirds. Their equation is based on data from six species but it is unclear how broadly it may be applied to other shorebirds. The American Woodcock (*Scolopax minor*) is an upland shorebird with life history characteristics different from most other shorebirds (Sheldon 1967). As part of a study on reproductive energetics of American Woodcock, we raised Woodcock in captivity and determined values for metabolic parameters; here we report measured values for basal metabolic rate (BMR), lower critical temperature (LCT), and standard metabolism below the thermoneutral zone (TNZ).

METHODS

American Woodcock (2 M, 3 F) were reared from eggs collected on the Moosehorn National Wildlife Refuge, Calais, Maine. From July through mid-September 1988, birds were housed in outside pens at ambient temperature and photoperiod at Orono, Maine. From mid-September 1988 until the beginning of experiments in November, birds were housed in individual cages in an environmental chamber which was maintained at constant 19°C air temperature. Photoperiod in the chamber was maintained at September levels (13:11, L:D) through December 1989, and then advanced gradually to normal levels following

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termination of the experiments. All birds used in the analysis had completed their post-juvenile molts. Birds were fed earthworms (*Lumbricus terrestris*) ad libitum and were handled daily and habituated to captivity (Vander Haegen et al. 1993a).

Metabolic rates were measured in a 4.6 l plexiglass metabolism chamber, during the resting phase of the birds' daily cycle and in complete darkness. Birds were fasted for 6 h prior to being placed in the chamber and were in a post-absorptive state. Oxygen consumption (VO_2) and carbon dioxide production (VCO_2) were measured in an open circuit system using a Beckman 755 O_2 analyzer and a Beckman 864 infrared CO_2 analyzer. Water vapor was removed from the air stream immediately downstream from the metabolic chamber. Flow rates were measured downstream from the metabolic chamber and ranged from 2.5 to 3.0 l/min. The system was calibrated to standard gas mixtures and zeroed to ambient air at the beginning of each run. Temperature in the metabolism chamber (T_a) and in the air stream at the entrance to the flow meter was measured with 28-ga thermocouples. Gas concentrations and temperatures were sampled every second by a CR21X micrologger (Campbell Scientific, Logan, Utah), averaged every 60 sec, and recorded by a microcomputer. T_a was controlled by placing the metabolic chamber in a walk-in environmental chamber.

Metabolism was measured at 2–3 temperatures per night, always proceeding from higher to lower temperature (Pohl 1969). Following a 1-h adjustment period at each temperature, gas concentrations were monitored for 30 min. VO_2 and VCO_2 were derived in two ways: first, by averaging the final 15 min of each trial; and second, by averaging ≥4 min of the lowest period of constant values obtained during each trial (both methods appear in the literature and could conceivably yield different results). VO_2 obtained by these two methods differed by only 2.3% at air temperatures >20°C. Therefore, we used the final 15 min to calculate metabolic rate. All gas volumes were corrected to standard temperature and pressure. Metabolism was calculated using equation 3b in Withers (1977). BMR for each bird was determined by averaging all values obtained from 23 to 30°C and assuming a conversion factor of 20.08 kJ per liter of O_2 consumed. LCT was determined as the point where the line representing BMR intersected the regression line for all points ≤20°C. Least-squares regression was used to evaluate the effect of temperature on metabolic rate below the TNZ. Means are reported ± 1 SE.

RESULTS

The mean BMR for 5 woodcock was 1.22 ± 0.18 ml O_2 $g^{-1}h^{-1}$. Table 1 compares BMR measured in this study to values predicted from published allometric equations. LCT was estimated as 22°C (Fig. 1). Below this temperature, the relationship between metabolic rate and ambient temperature was best described by the equation: $VO_2 = 2.047 - 0.0375(T_a)$, ($r^2 = 0.62$, N = 29). Mean mass of captive woodcock over all metabolic experiments was 156.7 ± 16.0 g.

When VO_2 for American Woodcock was set to zero, the regression of VO_2 on T_a (below LCT) extrapolated to a value of 55°C which is 15° above the average body temperature for birds (Calder and King 1974). This discrepancy indicates that, like many birds, American Woodcock vary their thermal conductance at ambient temperatures below the TNZ (Schmidt-Nielsen 1983:268).

TABLE 1

COMPARISON OF MEASURED AND PREDICTED BASAL METABOLIC RATE (BMR) IN THE AMERICAN WOODCOCK (VALUES FOR A 157 G BIRD)

	BMR (kJ day^{-1})	Measured relative to predicted (%)
Measured value (this study)	92.5	
Predictive equations		
Aschoff and Pohl (1970)[a]	79.0	+17
Lasiewski and Dawson (1967)[b]	85.9	+8
Kendeigh et al. (1977)[a]	94.3	−2
Kersten and Piersma (1987)[c]	113.4	−18

[a] Equations for non-passerines at night.
[b] Equation for non-passerines, day and night.
[c] Equation for shorebirds.

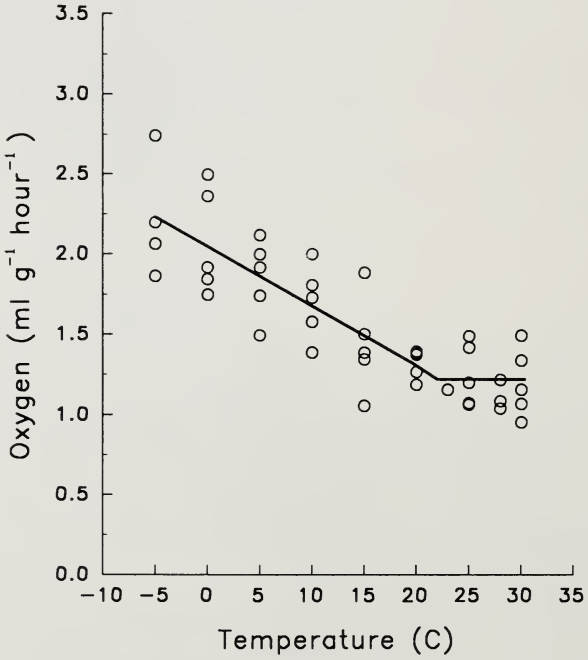

FIG. 1. Effect of ambient temperature on oxygen consumption by American Woodcock during the resting phase of their daily cycle (N = 2 males, 3 females).

DISCUSSION

Although BMR for American Woodcock was greater than that predicted by some generalized equations for non-passerines, it did not follow the elevated pattern for shorebirds predicted by the equation of Kersten and Piersma (1987) (Table 1). Other shorebirds, however, have been shown to follow this pattern of elevated metabolism. BMRs of Sanderlings (*Calidris alba*) (Castro 1987) and Pacific Golden-Plovers (*Pluvialis fulva*) (Mathiu et al. 1989) measured during the day were greater than those predicted by equations for the active phase or by more generalized equations for day and night (Castro 1987, Mathiu et al. 1989).

Two factors may have contributed to the differences between observed and predicted BMR in American Woodcock. First, the birds in our study were raised in captivity which may have affected their metabolic rates (Warkentin and West 1990). For example, our birds were conditioned to the laboratory environment, which likely reduced their apprehension during the experiments and increased the probability that they achieved a true resting state (Robbins 1983:107). Second, if BMR is associated with daily energy expenditure (DEE) as suggested by Kersten and Piersma (1987) and Daan et al. (1990), the differences in BMR between American Woodcock and other shorebirds may be related to differences in their natural history that influence DEE.

Kersten and Piersma (1987) argued that high BMR in shorebirds may be caused by increased use of skeletal muscles and their supporting abdominal organs at some point of high DEE in their yearly cycle (e.g., pre-migratory hyperphagia, migration, or winter cold periods). If this hypothesis is correct, American Woodcock should not encounter periods of energetic stress of the same magnitude as do other shorebirds. We know that conditions experienced by American Woodcock during early spring on the northern breeding grounds can be severe, with prolonged cold temperatures and periods of reduced food availability (Sheldon 1967, Vander Haegen et al. 1993b). Furthermore, female American Woodcock preparing to nest are active both day and night as they increase stored energy reserves prior to laying a clutch (Vander Haegen 1992). Although these conditions imply a high DEE during the breeding season for American woodcock, it is unlikely that Woodcock attain levels equal to those required of Arctic-nesting shorebirds.

Greater differences in DEE between American Woodcock and other shorebirds may occur during migration and in winter. American Woodcock migrate considerably shorter distances than do many shorebirds, and probably do not incur as high an energetic cost during the pre-migratory and migration periods. American Woodcock also differ from most shore-

birds by inhabiting forests, rather than coastal or grassland habitats where convection, and hence the potential for convective heat loss, is typically high. Therefore, the periods proffered by Kersten and Piersma (1987) as candidates for high DEE in shorebirds (i.e., "long-distance migration" and "wintering in unsheltered habitats") are probably less demanding energetically for American Woodcock than for other shorebirds. Although comparable measurements from other species of upland shorebirds are generally lacking, BMR of one European Woodcock (*S. rusticola*) measured by Gavrilov and Dol'nik (Kendeigh et al. 1977) was 21% below the rate predicted by the equation of Kersten and Piersma (1987), a value similar to the 18% differential reported here for American Woodcock. Like its North American congener, the European Woodcock inhabits forested habitats and migrates relatively short distances (Sheldon 1967).

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YELLOW-LEGGED GULLS (*LARUS CACHINNANS*) IN NORTH AMERICA

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ABSTRACT.—A specimen and two photographs of Yellow-legged Gulls (*Larus cachinnans*) are evidence of the occurrence of this species in North America. A description of a gull of definitive plumage, collected in the Madeleine Islands, Quebec, Canada, on 16 August 1973, previously has been published as that of a possible hybrid Herring Gull (*L. argentatus*) × Lesser Black-backed Gull (*L. fuscus*). Following detailed comparison to its suggested parent species and to *L. c. atlantis,* reassignment to this latter taxon is recommended, chiefly on the basis of the specimen's restricted but dense head-streaking and advanced primary molt in late summer, neither compatible with the other two species. A second occurrence in the winter of 1985 in St. Johns, Newfoundland, and a third in the winters of 1990–1993 in Washington, D.C., refer to two birds in definitive alternate plumage as early as January. Both had the large heads, sloped forecrowns, long, rather heavy bills, medium gray mantles, extensively black wing-tips, and bare-part colors characteristic of one of the two western subspecies (*atlantis* and *michahellis*) of *L. cachinnans.* Both photographic records have been reviewed by European consultants, the latter extensively so. *Received 18 Feb. 1993, accepted 15 Sept. 1993.*

Although the Yellow-legged Gull (*Larus cachinnans*) is not included in the avifauna of North America (American Ornithologists' Union 1983), its occurrence in the United States and Canada is documented by a specimen and by two sight records supported by photographs and field notes.

RECORDS

Quebec 1973.—The first Yellow-legged Gull in North America was encountered in the Madeleine Islands, Quebec, Canada, on 16 August 1973. The bird was collected, and the skin was deposited in the National Museum of Natural Sciences (now Canadian Museum of Nature), Ottawa (catalogue number 60750). Gosselin et al. (1986) published a full description of this individual, including key measurements and comparative photographs of the specimen with specimens of Herring Gulls (*L. argentatus smithsonianus*), *L. c. atlantis, L. c. michahellis,* and Lesser Black-backed Gulls (*L. fuscus graellsii*). Although the authors acknowledged that the bird was very similar to *L. c. atlantis* in virtually all respects, they concluded that it was possibly a hybrid, most probably of *L. a. smithsonianus* and *L. f. graellsii.* Either conclusion was compatible with the measurements of a male (Dwight 1925). The specimen could not be sexed because of damage, and worn outer primaries and molting rectrices prevented a precise measurement of the wing or a useful measurement of the tail. Their determination was apparently based on conjectural probability of occurrence, following Barth's suggestion (1968) that *atlantis* might be of hybrid origin, and on the specimen's wing pattern, in which "the black areas in the primaries seem less extensive [than in *atlantis*]."

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FIG. 1. (top to bottom) *Larus fuscus graellsii,* USNM 421801, female, Green Run, Maryland, 7 October 1948; *L. cachinnans atlantis,* NMNS 60750, unsexed, Iles-de-la-Madeleine, Quebec, 16 August 1973; *L. c. atlantis,* USNM 264097, female, Pico, Azores, 17 August 1921; *L. argentatus smithsonianus,* USNM 57546, male, Yukon Territory, 21 July 1972.

In the course of research related to the 1990–1993 record (discussed below), we examined a skin of *L. c. atlantis* in the U.S. National Museum (USNM 264097) collected in the Azores on 17 August 1921, 52 years earlier almost to the day than NMNS 60750. The published photographs and description of 60750 showed that the two birds were strikingly alike, and a direct comparison was arranged.

E. K. Barth (fide Gosselin et al. 1986) had measured the darkness of the mantle of 60750 as 4.5 on the Munsell scale, precisely matching his measurement of *atlantis* (the darkest of the *L. cachinnans* subspecies), and our visual comparison of it with 264097 and with specimens of the paler *L. c. michahellis* reinforced this assessment (Fig. 1). Though not reflected in the score, equally obvious to the eye was the lack of any brownish tone to the mantle color on either bird when compared to that of *graellsii,* a character noted by Dwight (1922) in the description of *atlantis*: "Compared with *affinis* [=*graellsii*], the nearest race [of *L. fuscus*] both in color and distribution, the mantle of *atlantis* is a clearer, paler, bluer gray without any of the brownish tinge that marks all the other races even in perfectly fresh plumage."

Also identical on 60750 and 264097, both in shade and distribution, was the dense, sharp, rather uniformly dark head streaking (Fig. 2) covering all but the chin and throat and darkest around the eyes, a mark of definitive basic plumage characteristically acquired by *L. cach-*

FIG. 2. (left to right) *Larus fuscus graellsii,* USNM 421801, female, Green Run, Maryland, 7 October 1948; *L. cachinnans atlantis,* NMNS 60750, unsexed, Iles-de-la-Madeleine, Quebec, 16 August 1973; *L. c. atlantis,* USNM 264097, female, Pico, Azores, 17 August 1921; *L. argentatus smithsonianus,* USNM 57546, male, Yukon Territory, 21 July 1972.

innans in August. Head streaking is not obvious in either *L. a. smithsonianus* or *L. f. graellsii* until later in the year, adults of these two taxa typically developing their winter head patterns to full intensity during September and October (pers. obs.). In comparison to the two specimens, the head streaking of *graellsii* is similar in average darkness and sharpness, but usually somewhat more extensive; that of *smithsonianus* is paler, coarser, and less restricted, extending onto the breast in the form of mottled spotting; that of *michahellis* tends to be more restricted and less dense than that of *atlantis* except around the eye, often given the impression of a predominantly white head (Vercruysse 1984).

The advanced stage of primary molt also pointed to some form of *L. cachinnans* (Mayaud 1940, De Mesel 1990; on 60750 p8 was nearly full-grown, p9 was half-grown, and p10 had not yet been shed, giving a molt score of 42. Molt was less advanced on 264097 in which p6 was nearly full-grown, p7 was partially grown, and p8 to p10 had not been shed, giving a molt score of 32. On six other *atlantis* skins collected on 6 and 7 September, molt scores ranged from 34 to 42. In contrast, *argentatus* and *fuscus* adults typically complete primary molt between October and December (Cramp and Simmons 1983) and attain mid-August molt scores of less than 30 and less than 20 respectively (Harris 1971, Barth 1975a, Verbeek 1977, Walters 1978, Vandenbulcke 1989). No molt studies of *smithsonianus* have been published, but none of fourteen adults collected between 15 July and 27 August have a molt score higher than 24, and none collected before 20 November have completed primary molt.

Gosselin et al. (1986) explained the early primary molt in 60750 as that of a bird acquiring fourth-winter plumage—that is, attaining definitive Basic plumage for the first time—a hypothesis suggested to them by an incomplete black band on the bill. There is no other trace

of immaturity, however; and older, otherwise fully adult *L. cachinnans* (as well as other large gulls) in definitive basic have been seen with dark bill markings (Géroudet 1992). The old rectrices and outer primary coverts lack the brown or black markings typical of Basic III plumage. In addition, the heavily worn tenth primary of 60750 is black, not brown like an old third-year outer primary in August, and the large white subapical spot on that feather suggests that the bird was already in definitive basic plumage after its previous prebasic molt.

Harris et al. (1978), working in gull colonies off the Welsh coast, found three definite *L. a. argenteus* × *L. f. graellsii* hybrids recognizable by "a mid-grey mantle, pale yellow legs, and an orange-yellow eye-ring during the breeding season." The orange-red orbital ring and yellow legs of 60750 are characteristic of both *L. cachinnans* and *L. fuscus.*

With respect to the black areas on the primaries, several elements were evaluated: the black-and-white patterns at the tips of p10 and p9, the extent of black on the inner webs of p10 to p7, and the innermost primary with black.

On 60750 the large white mirror on p10 is separated from the white tip by a complete black band, and p9 lacks a mirror altogether. These patterns, both showing maximum black for *L. argentatus, L. cachinnans,* and *L. fuscus,* are common for both *atlantis* and *graellsii* and somewhat less common for *michahellis* (De Mesel 1990) and *smithsonianus* (found on 21 out of 72 specimens). (The skins of two *argentatus* × *fuscus* hybrids at the National Museum of Natural History, Leiden—RMNH 6818 and 33314—both have mirrors on p9; note, however, that the *L. argentatus* parent would not have been *smithsonianus* in these cases.)

P9 on 60750 had not grown out far enough for exact analysis of its inner web, but p10–p7 were assessed by using Tp values—a measure of the extent of black defined by Devillers and Potvliege (1981) as the distance from the distal tip of the gray tongue on the inner web to the proximal edge of the white tip. Tp 10 was measured at 178 mm; Tp9, all black from the sheath to the white tip, at 116, Tp8 at 60 mm, and Tp7 at 30.5 mm. The value for Tp10 exceeded the mean for *atlantis* by 20 mm and the exposed Tp9 value was 2 mm greater than the mean for that feather. Values for both Tp8 and Tp7, however, are below the measured range for all but one of 41 *atlantis* specimens examined: on a skin at the British Museum of Natural History (Tring), BM 1913.10.22.230, Tp8 = 45 and Tp7 = 24, whereas on the other skins the range for Tp8 was 68–168 and that for Tp7 was 31–67 (Wilds, unpubl. data). The two latter Tp values for 60750 are compatible with a *smithsonianus* × *graellsii* hybrid. The extent of black on the four outer primaries of 60750 relative to that on average wingtips of male *atlantis, michahellis,* and *smithsonianus* is illustrated in Fig. 3.

The fourth primary on the right wing is broken off near the base, but on the left wing it is intact and marked by a black spot on the outer web, as are the fifth primaries on both wings. This pattern (black to p4) is the most common one for *atlantis* and *graellsii,* and nearly as common on *michahellis,* but unusually extensive for *smithsonianus* (found on 10 out of 72 specimens).

Thus, the Tp8 and Tp7 values are lower than expected for *atlantis,* but within the range of the limited number of specimens studied. These low values do not seem large enough to dismiss the otherwise perfect match of 60750 with *atlantis* in respect to mantle color, wing-tip pattern, head pattern, soft-part colors, biometrics (though incomplete), and especially stage of molt. Only wing-tip pattern and biometrics are equally compatible with a possible hybrid (although some other features are within the range of the two hypothesized parent species). We therefore propose that NMNS 60750 be considered the first specimen of *L. cachinnans* taken in North America.

Newfoundland 1985.—The first sighting of a Yellow-legged Gull in North America was

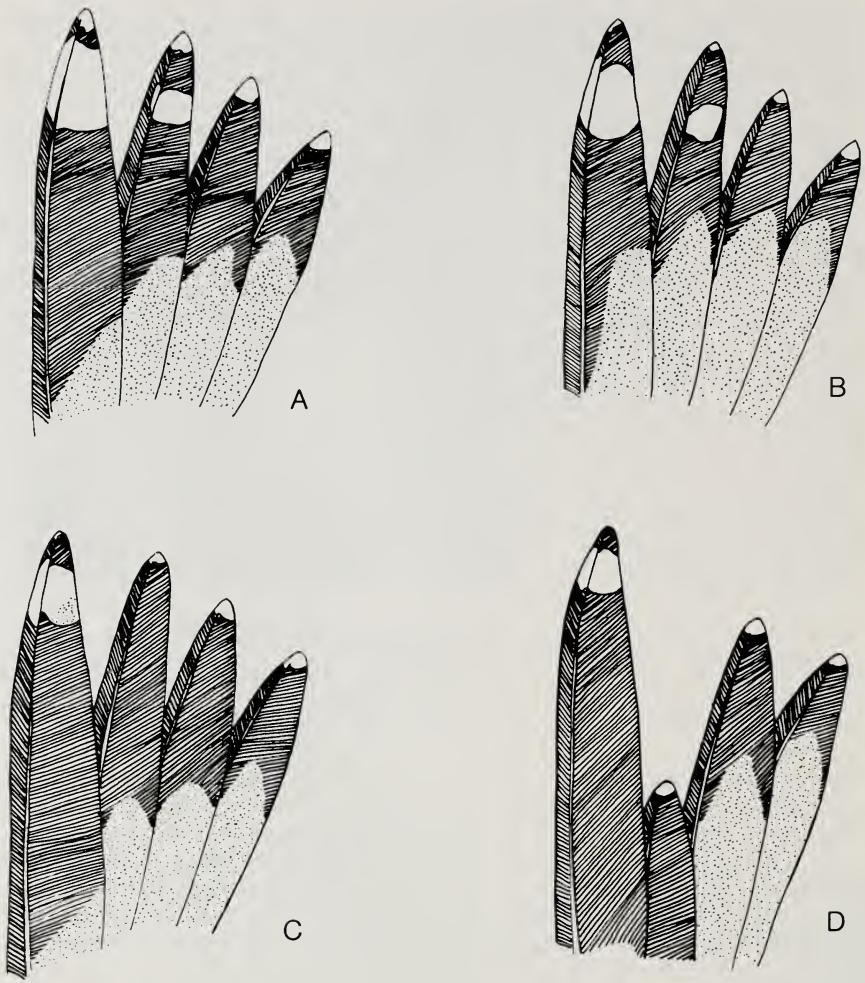

FIG. 3. Underwing patterns showing the mean extent of black on the inner webs (Tp values) for primaries 10–7 in (A) *L. cachinnans michahellis,* (B) *L. a. smithsonianus* and (C) *L. c. atlantis,* and the actual distribution of black on p10–p7 on (D) *L. c. atlantis* NMNS 60750. Drawing by Claudia Angle.

made in Newfoundland in 1985 by Bruce Mactavish (Heil 1985). That bird, in definitive alternate plumage, was present at St. John's from 16 January to 15 April and was described in field notes and photographed, but neither the description nor the photographs were published. According to the notes, the size was similar to that of a Herring Gull, but the head and bill were more massive than in that species. The orbital ring was dull crimson, the legs dull yellow, and the eye yellow. The mantle was slate gray, intermediate between *smithsonianus* and *graellsii* but perhaps closer to the latter. The black of the wing-tip was more

extensive than on a Herring Gull, reaching at least p5 and nearly reaching the tips of the greater coverts on p7–p10. It had a large mirror on p10, separated from the white tip by a complete black band, and a small mirror on p9. The record was examined by the late Peter J. Grant, who expressed the opinion that the bird would have been judged a representative of the subspecies *michahellis* if it had been seen in England (Mactavish, pers. comm.).

Washington, D.C. 1990–1993.—On 1 February 1990, an adult Yellow-legged Gull was discovered by David Czaplak at Georgetown Reservoir in Washington, D.C. It remained until 7 February and was photographed in color. Detailed notes were taken by Czaplak, Claudia Wilds, Robert Hilton, and Willem Maane. Presumably the same individual (identical in size, proportions, coloration, and especially wing-tip pattern) was present at the reservoir, or at a landfill in nearby Laytonsville, Maryland, from 18 December 1990 to 21 March 1991, again from 26 December 1991 to 23 February 1992, and from 8 January to 28 March 1993.

The bird was studied at length on numerous dates under diverse lighting conditions. Distance from the observers at the reservoir varied from 20 m to 60 m. Present for comparison were adult Great Black-backed (*L. marinus*), Herring (*L. a. smithsonianus*), Lesser Black-backed (*L. f. graellsii*) and Ring-billed gulls (*L. delawarensis*). The following description is based on the notes and photographs of the above-mentioned observers, as well as those of Mary Gustafson, Ottavio Janni, Michael O'Brien, and Paul O'Brien, taken in 1990, 1991 and 1992.

Plumage.—The bird was, variably, in complete or nearly complete definitive alternate plumage, with entirely white tail and underparts. On the white head some observers noted a few faint, narrow streaks of gray on the forehead above the lores and above and behind the eye, as well as a very faint, diffuse spot of gray in front of the eye. These markings were present in December but usually absent by late January. Under most conditions, the head appeared immaculate.

The mantle was medium gray, distinctly darker and ashier than that of *smithsonianus* and distinctly paler and more bluish than that of *L. f. graellsii,* lacking its brownish tinge. Under most conditions, it appeared to observers to be closer in tone to *smithsonianus* than to *graellsii* (like *michahellis*), although it seemed relatively darker in late afternoon light or on overcast days. (The photographs, most of which were taken late in the day or on dark days, usually indicated a darker mantle closer to that of *graellsii* than to *smithsonianus* [like *atlantis*].) The white tips to the tertials and rearmost scapulars were narrower than on *smithsonianus* and formed thinner white crescents on the folded wing.

Only p10 had a white mirror. This was rectangular and covered both webs from edge to edge. It was completely separated from the white tip by a narrow black band less than one-fifth as long as the mirror. Primaries 8–10 were black on the outer webs almost up to the base. On the inner webs of p8–p10, a gray tongue extended roughly half-way from the base to the tip. These tongues were the same shade of gray as the mantle; they contrasted less with the black than on *smithsonianus.* P7 showed black on the outer web more than half-way to the base and black on the inner web for only a short distance, with the gray tongue on this web forming a distinct U shape. There was a diffuse paler border separating the gray of the U from the black. P6 was black on the outer web less than a third of the way to the base, and the black on the inner web was about half of the outer in length. P5 had a narrow black band across both webs, slightly wider on the outer web and only slightly wider than the white tip. There was a small black spot on p4, on the outer web only.

This distribution of black on the primaries resulted in a wing-tip showing much more black than in *smithsonianus,* with the black at the proximal ends of p6–10 forming an almost straight line across the wing nearly perpendicular to the trailing edge. On *smithsonianus* the gray of the mantle makes a much more noticeably convex intrusion into the black of the

wing-tip. On *graellsii* the extent of black is roughly similar to that on *L. cachinnans,* but there is much less contrast between the black and the dark gray of the mantle. These differences in the shape of black in the wing-tip among the three forms were seen quite easily during preening or in flight.

The underside of p10 showed the white mirror as on the dorsal surface, a black outer web, and a dark gray inner web. The rest of the primaries, as well as the secondaries, formed a gray subterminal band across the spread wing when seen from below. This pattern was quite different from the pale underwing of *smithsonianus* and somewhat paler than the dark underwing bar of *graellsii.*

Bare parts.—The iris was pale yellow. The orbital ring was an intense orange-red to vermilion, brighter and much more noticeable than in *smithsonianus.* It was not quite as deep a red as on *delawarensis* in alternate plumage. The bill had a large, bright red spot at the gonydeal angle, extending slightly onto the upper mandible. The tip was pale creamy yellow, and the rest was deep yellow to orange-yellow, depending on lighting conditions. The bill was much brighter than on most adult *smithsonianus* in January and February, and slightly deeper yellow than in those *smithsonianus* already reaching definitive alternate plumage. The legs and feet were a rich orange-yellow to pure, bright yellow, also depending on lighting conditions. Both the bill and legs were a richer, deeper yellow than on winter *graellsii.*

Size and structure.—The bird was about the same size overall as an average *smithsonianus.* Size impression depended on posture. The relatively large head and strong bill made the bird look slightly larger than a Herring Gull when alert, whereas at rest it looked about the same size or even slightly smaller. It was slightly more broad-chested when viewed from the front, and its stance was typically more horizontal than that of *smithsonianus.* It was not nearly so stout-bodied as *marinus,* and it lacked *graellsii*'s attenuated rear end.

The most distinctive structural differences were in the head and bill. Compared to *smithsonianus,* the head was both broader and longer. The forehead made a flatter angle with the bill and sloped more gently to the crown. The forehead, crown, and nape were more gradually curved, giving a more domed appearance to the head. The head shape was thus intermediate between *smithsonianus* and *marinus.* It did not in any way suggest *graellsii,* which has a narrower head, a sharper angle between the bill and forehead, and a much more squared-off crown and nape.

The bill was slightly longer than average for *smithsonianus* and marginally thicker as well. The gonydeal angle was slightly more prominent, and the tip was more square-ended. These features combined to give a distinctly heavier bill than in *smithsonianus* but still lacking the massive look of *marinus.*

Impressions of the bird in flight were brief, but the overall effect was distinctive. The wings were slightly broader and longer than *smithsonianus.* They lacked the long, narrow look of *graellsii.*

Evaluation of the record.—In response to requests by the Maryland/D.C. Records Committee, seven written opinions (two of them joint opinions) on the identity of the gull were obtained from W. R. P. Bourne, Alan Dean, Dirk De Mesel, Philippe J. Dubois, Paul Holt, W. Hoogendoorn, R. A. Hume, Norbert Roothaert and Pierre Yésou.

All agreed that the Georgetown bird belonged to *Larus cachinnans* (*sensu* Haffer [1982]), primarily on the basis of the combined characters of head- and bill-shape, bare-parts colors, mantle color, and extent and distribution of black in the wing-tips; some also mentioned the underwing pattern and minimal head streaking. Hume specifically stated that it was "not in the least like northern *argentatus* as we see them in the U.K. in winter." Most were cautious about pinpointing the exact subspecies, but several narrowed the choice to the two races of southwestern Europe, *L. c. atlantis* or *L. c. michahellis* or preferred one or the other.

The diversity in plumage and bare-parts colors among North American Herring Gulls, occasionally including yellow legs (Dwight 1925), may well have prevented earlier detection of *L. cachinnans* vagrants. On the other hand, the expansion of *L. c. michahellis* as a breeding bird west and north of the Mediterranean and as a post-breeding migrant north to 53°N is a very recent phenomenon. It is only in the 1980s and 1990s that the field characters for this subspecies (in definitive and juvenile plumages only) have been fully analyzed and published (especially Devillers and Potvliege 1981; Devillers 1983; van den Berg 1983; Dubois and Yésou 1984; Grant 1984, 1986; Harris et al. 1989; De Mesel 1990), and most of this literature is so little known in North America that some gullwatchers are still likely to regard a claimed sighting as presumptuous.

The occurrence of *L. c. atlantis,* considered a largely sedentary taxon, is less explicable. It should be noted, however, that the colonies in the western Azores, at 39°N, 31°W are due east of Delaware and due south of Greenland and thus far closer to North America than any other populations of *L. cachinnans.* Much less is known about its possible movements, perhaps because of the lack of banding or color-marking programs, and because of its similarity to *michahellis* when the two cannot be directly compared.

IDENTIFICATION

Although the yellow-legged gulls of Asia remain poorly known, they are now increasingly under study (e.g., Filchagov et al. 1992). Research on the European forms has exploded in the last twelve years and is continuing. Those familiar with both groups find them very different from each other.

The three European forms that have been assigned by all authors from Vaurie (1965) to the present (except for Barth 1968) either to *L. cachinnans* or to the *cachinnans* group of *L. argentatus*—nominate *cachinnans, michahellis,* and *atlantis*—have well-defined structural characters and color patterns that should make them readily identifiable in definitive plumage as to species and sometimes to subspecies.

All have a proportionately longer, heavier bill and bulkier head and body than *L. argentatus* or *L. fuscus.* All have a yellow bill with a red gonydeal spot, both colors typically brighter than in the other two species outside breeding season. All have an orange-red to vermilion orbital ring and yellow legs. All have a mantle paler than that of *L. f. graellsii* and darker than that of *L. a. argenteus.* On the underwing, the inner primaries and secondaries consistently form a broad gray subterminal bar. The black on the primaries extends inward to at least p5 and often to p4. All complete molt into definitive basic plumage earlier than the other two species: the head and body by early September and the primaries by late October at the latest. In basic plumage, head-streaking is much more restricted than on any subspecies of *L. argentatus* and is normally hard to see at any distance by early winter.

Of the three subspecies, *atlantis* should be the easiest to recognize (when in the company of other gulls) as some form of *L. cachinnans*

because of the color of its mantle, similar to that of a Laughing Gull, *L. atricilla,* and perceptibly lighter than that of *L. f. graellsii,* and its size, averaging smaller than *L. a. smithsonianus* and *L. c. michahellis* and slightly larger than *graellsii.* The wing-tip is extensively dark, with the slate-gray tongue on primaries 7–10 separated from the white tip by an increasingly wide (from p7 to p10) band of black (Mayaud 1940) forming a large black triangle. Tp values average 60% greater than for *smithsonianus* (Wilds, unpubl. data; Fig. 3). The ninth primary lacks a white mirror except in the Canary Islands population, where a small mirror is sometimes present (Devillers, in Cramp and Simmons 1983).

Nominate *cachinnans* is much more like *L. a. smithsonianus* in size and mantle color. The legs vary from "rather bright" yellow in the western Black Sea population (W. Hoogendoorn and Philippe J. Dubois, pers. comm.) to pale straw-yellow farther east (Nitecki, fide Chylarecki and Sikora 1991. Dubois suggests that this variation may be seasonal.) On the fully extended wing (as in flight or when landing), the long white (or very pale gray) tongue on the inner webs of p10 and p9 should be prominent from below, contrasting with the black outer web and band above the tip. P10 usually has a long white tip with no black band across it, or with at most an incomplete black band. P9 always has a mirror, often a large one extending from edge to edge of the feather (Kohl 1958, Mierauskas and Greimas 1992). Tp values are not available for this subspecies. If banding records are indicative (De Mesel 1990), this subspecies rarely reaches western Europe. (Only two recoveries west of Denmark—one in Germany and one in France—were reported through January 1990).

Larus c. michahellis is equal in size to *L. a. smithsonianus* or a little larger. Its mantle color is perceptibly darker in the field, between the shade of *smithsonianus* and that of a California Gull, *L. californicus californicus* (*sensu* Jehl 1987) and always obviously darker than Ring-billed Gull, *L. delawarensis.* The wing-tip pattern is distinctive. As in *atlantis,* the black on p10, p9, p8, and p7 extends well up the feathers, forming a large black triangle with the inner edge nearly straight-edged rather than crescent-shaped as in *smithsonianus.* The Tp values for p7–10 average 40% greater than for *smithsonianus* (De Mesel 1990; Wilds, unpubl. data; Fig. 3). The gray tongue above the black on the inner web of the outermost primaries is approximately the same shade as the mantle and inconspicuous. On p10, the tip pattern varies from being all white to showing a complete black subterminal band that defines a large mirror. On the majority of individuals, there is a mirror on p9; in Belgium, for example, 58.5 percent of captured females and 67 percent of captured males had a mirror on that feather (De Mesel 1990).

Although the juvenal plumage of *michahellis* is explained and illus-

trated by Dubois and Yésou (1984) and Harris et al. (1989), predefinitive plumages of *L. cachinnans* have not yet been fully described.

Several western Palearctic populations of gulls with yellow legs continue to cause puzzlement and controversy, and a vagrant from one of these groups might be easy to overlook and difficult to identify. It is unclear whether the birds that breed on the Atlantic coast of southern Morocco should be assigned to *michahellis* or *atlantis* or are intermediate between the two taxa. Specimens from this population have not been found in the museums we visited. There are no descriptions of these birds in the literature, and nothing is known of their movements. The Iberian "Cantabrican Gull," found on the Atlantic coast of Spain and possibly Portugal, is currently assigned to *michahellis* but, like *argenteus,* is a smaller, paler gull with proportionately shorter legs and a thinner bill (Joiris 1978; Teyssèdre 1983, 1984; Carrera et al. 1987; Dubois 1987). The Baltic "*omissus*" is thought by some to be a subspecies of *l. cachinnans* (e.g., Haffer 1982), by others to be a possible subspecies of *L. argentatus* (e.g., Mierauskas et al. 1991), and by still others to be no more than a variant of nominate *argentatus* (e.g., Barth 1968, 1975b). The yellow-legged individuals among the Herring Gulls *L. a. argentatus* of the Baltic and Scandinavia, including (or as well as) "*omissus,*" differ structurally from *L. cachinnans* in having a shorter, thinner bill (Mierauskas et al. 1991). The wing-tip pattern lacks the extensive black on p7, p8, and p9, and thus the filled-in triangle (Devillers and Potvliege 1981), and might not be separable from that of a yellow-legged *smithsonianus* in the field, though p9 and p10 frequently show much more white on nominate *argentatus.* The mantle may be as dark as *michahellis* or as light as *smithsonianus.* In winter the bare parts are faded and dull, as in *smithsonianus.* Both the "Cantabrican Gull" and "*omissus*" have "long calls" much more like that of *L. argentatus* than like that of *L. cachinnans* (Teyssèdre 1984, Mierauskas et al. 1991).

A yellow-legged representative of *L. a. argentatus* could conceivably reach North America; the subspecies is found all around the shores of the North Sea, the English Channel, and the Atlantic coast of continental Europe in winter, including inland roosts, but is scarce on the west coast of Great Britain (Stanley et al. 1982, Coulson et al. 1984).

On the basis of the three individuals reported here, however, we expect that the two western subspecies of *L. cachinnans—atlantis* and *michahellis*—are the vagrant gulls with yellow legs most likely to be noticed if they find their way to the east coast of North America.

We hope that the publication of these details will improve the chances that Yellow-legged Gulls reaching North America will be recognized, closely examined, and satisfactorily documented.

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BEHAVIOR OF HORNED GUANS IN CHIAPAS, MEXICO

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Abstract.—Behavior of Horned Guans (*Oreophasis derbianus*) in the El Triunfo Biosphere Reserve, Chiapas, Mexico, from February to May in 1982 and 1983, including preening, dustbathing and foraging behavior during the breeding season, is described. Horned Guans devote most of their daytime activity to preening and comfort behavior. To dustbathe, they use treefall gaps and only bathe once a day. Dustbathing seems to be an important factor during courtship. Horned Guans are mainly arboreal and consume mostly fruits and green leaves. *Received 13 April 1993, accepted 1 Sept. 1993.*

Most populations of the Horned Guan (*Oreophasis derbianus*) are imperiled as a result of intense hunting and rapid destruction of the cloud forest in the species' restricted geographical range in southern Mexico and Guatemala (Collar et al. 1992). Behavioral and ecological information about the Horned Guan, however, is scanty. A few studies deal with the taxonomy and distribution of this species (e.g., Ridgway and Friedmann 1946, Friedmann et al. 1950, Andrle 1967, Vaurie 1968, Blake 1977, Binford 1989). There are published observations about the species in the field and in captivity (Sclater and Salvin 1859, Salvin 1860, Salvin and Godman 1902, Wagner 1953, Andrle 1967, 1969a, b, Delacour and Amadon 1973, Alvarez del Toro 1976, Parker et al. 1976, Delacour 1977, Estudillo 1979). However, there is little field information concerning its behavior and natural history (see Andrle 1967; González-García 1984, 1988). Here I provide detailed observations on preening, dustbathing, foraging, and other behaviors of Horned Guans in the Sierra Madre de Chiapas during the breeding season.

STUDY SITE AND METHODS

I made all observations in core area "I" of the El Triunfo Biosphere Reserve, Chiapas, Mexico (Cerro El Triunfo, 15°35′–15°45′N, 92°41′–92°53′W). This core area covers 11,594 ha; elevation varies from 1000 to 2500 m above sea level. Cloud forest occurs within a range of elevations from 1600 to 2450 m, and the study site itself is at 1850 m. González-García (1984), Long and Heath (1991), Williams (1991), and Ramírez and González-García (unpubl. data) provide information on vegetation and climate there. The vegetation is extremely humid and relatively undisturbed cloud forest, with the average annual precipitation exceeding 4000 mm. The mean annual temperature is 18°C, with little annual variation (González-García, unpubl. data).

Field work was conducted during the dry part of the year (February–May) in 1982 and 1983. During eight months of field work, I made daily observations lasting from 30 min to

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10 h, depending on ease of observation and weather. I used 10 × 40 binoculars, with or without a blind, at distances ranging from 5 to 35 m. Observations detailed here are based on ten individual Guans recognized on the basis of plumage, location, and horn size.

RESULTS AND DISCUSSION

Preening.—Observations were made at trees where Horned Guans were feeding or resting and at dust bath sites. Preening occurred throughout the day but especially at midday. Long sessions of preening (N = 16) lasted an average of 1.57 ± 0.48 h (SD). Preening is done by both male and female while they are on thick branches. Wings, breast, back, rump, and tail feathers can be cleaned and arranged while the bird is either standing or sitting on the branch, but scratching the face and preening the belly and tarsus feathers can be performed only while standing (the latter, by arching the back slightly and simultaneously lowering the tail to enable the beak to reach the parts that require preening). After preening, the bird shakes itself while standing, often flapping or fully spreading its wings and stretching its neck up and forward.

The Horned Guan generally devotes most of its time to the care and cleaning of its plumage. For example, during 8 hours of observation, a male devoted 6 h to preening and comfort behavior and 2 h to feeding. Horned Guans spend more time attending the back and wing feathers than those of any other part of its body. The order of importance of different body parts with respect to preening and comfort behavior is back and sides (for each, N = 13), wings (N = 9), spreading wings (N = 7), breast (N = 3), belly (N = 3), and tail (N = 3). Only a small proportion of preening involves scratching the head. Sometimes, after a preening session, a guan will expose its plumage to the sun, possibly for the purpose of removing ectoparasites or to dry itself.

Wing feathers are preened from above and below by spreading the wings slightly and running the beak along each feather from base to tip. The tail is preened in the same way. To preen its tail, back, and rump, the bird lowers its wings slightly and raises its tail.

Another observed comfort behavior is the backward spreading of one the of the wings and simultaneously stretching of the leg on the same side of the body. This behavior was observed after resting, preening, bathing, and after a long time spent incubating eggs.

Dust bathing.—The dust bath is characteristic of many galliform birds, including the Cracidae. The dust bath is believed to remove parasites, to keep feathers in good condition, and to maintain the optimum amount of oil in the plumage (Campbell and Lack 1985). In the Horned Guan, it may have the additional function of strengthening the pair bond during

courtship; the male often calls its females to the dustbath during courtship, and the nest site is later chosen in a nearby spot.

I found a dust bath site near the Palo Gordo trail (1.5 km west of the El Triunfo station) by following a pair of Horned Guans for 14 days. To bathe, birds use treefall gaps where the sun reaches the forest floor and dries the soil. The dust bath was relatively small at first, but increased in size with continuous use. The birds used the nearby vegetation, including medium-sized trees, bushes, and the branches and roots of the fallen tree that created the gap, as perches before and after bathing. Subsequent field observations indicate that the site used as a bath in 1982 and 1983 was not used in the following years. This suggests that the search for and establishment of new bathing sites may be an important factor during courtship.

Horned Guans usually bathe once, and occasionally two times, a day. Bathing is usually done between 12:00 and 16:00 h (once 10:00 h; N = 13), possibly owing to the fact that this is the time when the sun can penetrate the tree canopy most easily, and therefore dry the soil and make it most useful to the birds.

The Horned Guan may bathe alone or with its mate. In the former case, the bird glides silently to branches near the bath, descends to the ground and then walks to the site. On arriving, the bird first scratches the surface of the soil with its feet, making small turns, and then settles on the soil. It supports itself on one side and tosses up soil with the foot and wing on the other side. On finishing, the bird shakes itself three to four times in the bath or on a nearby branch where it then preens. After preening, the bird stretches out its wings until they are at right angles to its sides and sunbathes. From its perch the bird may go down to the ground to eat green leaves or small stones and to sun itself in the aforementioned position.

When bathing with a mate, the male always arrives first, tramples the site with his feet, and then "moos" to attract the female to the site. When the female arrives, the male withdraws briefly and the female begins to bathe, using the technique described above. Meanwhile, the male, standing to one side of the bath, arranges his plumage. When the female finishes and leaves in order to arrange her plumage and eat green leaves and small stones, the male enters the dust bath, bathes and then perches on a branch and begins preening. After both birds have bathed, the female is fed with green leaves by the male and emits calls that sound like guurk, guurk, guurk. On five occasions, a female that was close to a male at the dust bath, was observed to approach the male who had a piece of green leaf in its beak, even though he was not calling.

Single individuals bathe for several minutes ($\bar{x}$ = 29.6 ± 1.1 min, N

TABLE 1

LIST OF FAMILIES AND SPECIES OF PLANTS CONSUMED BY THE HORNED GUAN

Families[a]	Species	Plant type	Fruit morphology
Aquifoliaceae	*Ilex tolucana*	Lower midstory tree	Drupe
Araceae	*Anthurium* sp.	Epiphytic	—[c]
Araliaceae	*Dendropanax populifolius*	Higher upperstory tree	Drupe
	D. pallidus	Lower upperstory tree	Drupe
	Oreopanax capitatus	Epiphytic and higher midstory tree	Drupe
Cactaceae	*Epiphyllum crenatum* var. *crenatum*	Epiphytic	Berry
Cloranthaceae	*Hedyosmum mexicanum*	Higher midstory tree	Aggregate drupe[b]
Compositae	*Eupatorium chiapense*	Lower understory (herbaceous)	—[c]
	Schistocarpha bicolor	Higher understory (herbaceous)	—[c]
Lauraceae	*Nectandra reticulata*	Higher upperstory tree	Drupe
	Ocotea chiapensis	Higher midstory tree	Drupe
	O. matudai	Higher midstory tree	Drupe
	O. uxpanapana	Higher midstory tree	Drupe
	Licaria alata	Higher midstory tree	Drupe
	Persea liebmanii	Lower upperstory tree	Drupe
	Persea sp.	Lower upperstory tree	Drupe
	Phoebe bourgeauviana	Lower midstory tree	Drupe
	P. siltepecana	Lower upperstory tree	Drupe
Liliaceae	*Smilax jalapensis*	Hemiepiphytic vine	Berry
	S. lanceolata	Hemiepiphytic vine	Berry
	S. mollis	Hemiepiphytic vine	Berry
	S. purpusii	Hemiepiphytic vine	Berry
	S. subpubescens	Hemiepiphytic vine	Berry
Melastomataceae	*Conostegia volcanalis*	Lower midstory tree	Berry
	Miconia globulifera	Lower midstory tree	Berry
Moraceae	*Morus insignes*	Lower upperstory tree	Aggregate drupe[b]

TABLE 1
CONTINUED

Families[a]	Species	Plant type	Fruit morphology
Myrsinaceae	*Ardisia cucullata*	Lower midstory tree	Drupe
	A. compressa	Lower midstory tree	Drupe
Polemoniaceae	*Cobaea scandens*	Hemiepiphytic vine	—[c]
Rhamnaceae	*Rhamnus capraefolia* var. *grandifolia*	Higher midstory tree	Drupe
Solanaceae	*Cestrum* aff. *guatemalense*	Lower midstory shrub	Berry
	Solanum sp.	Hemiepiphytic vine	Berry[c]
Symplocaceae	*Symplocos hartwegii*	Lower midstory tree	Drupe
Ulmaceae	*Trema micrantha*	Higher midstory tree	Drupe
Urticaceae	*Urera alceifolia*	Lower midstory tree	Aqueno
	U. caracasana	Lower midstory tree	Aqueno
Verbenaceae	*Citharexylum mocinnii*	Higher midstory tree	Drupe

[a] Listed alphabetically, not systematically.
[b] The bird take bites from the aggregate fruit, each bite containing many fruitlets.
[c] Leaves of these species are consumed.

= 5), and members of a pair each spend an average of 17.5 ± 2.6 min bathing (N = 10).

Frugivory and foraging behaviors.—I marked all trees, shrubs and herbs used by Horned Guans and collected samples of leaves and fruits of plants consumed. All plants were identified by Ismael Calzada and Fernando Ramírez from the Instituto de Ecología herbarium. I also collected seven droppings from dustbathing sites.

I have observed Horned Guans consuming the fruits of 37 plant species from 18 families and the green leaves of five species (Table 1, including field data up to 1991), but I have never observed Horned Guans eating small vertebrates and only very rarely invertebrates, which other cracids are reported to do (see Sick 1970, Delacour and Amadon 1973, Estudillo 1979, Sermeño 1986). One fecal sample contained three undigested white larvae, which I suspect were consumed in a parasitized fruit. Food is mostly fruits from lower and higher midstory trees, followed by fruits and leaves of epi- and hemiepiphytes at these same levels. Drupes (21 species) and berries (10) are favored (Table 1). With the exception of *Hedyosmum mexicanum* and *Morus insignes,* fruits which were consumed in consecutive bites, other fruits were swallowed whole. Most of these species are commonly found along streams and ravines and on gently sloping hills. The four most common fruits consumed in 1982 and 1983 were *Nectandra reticulata* (N = 35), *Conostegia volcanalis* (N = 22), *Citharexylum mocinnii* (N = 18), and *Morus insignes* (N = 17). The seven fecal samples contained only fruit remains and seeds. Seeds in the fecal samples appeared intact, suggesting that Horned Guans may be important seed disseminators in the cloud forest.

Horned Guans acquired fruit either by reaching or gleaning (sensu Remsen and Robinson 1990), although the former tactic was more common (87.3%, N = 62). Birds arrived at fruiting trees and walked or jumped among branches in search of fruit. Horned Guans fed preferentially from the center of trees, stretching their legs and neck to reach fruit located in the periphery.

Feeding periods lasted 15–20 min ($\bar{x}$ = 15.7 ± 4.9 min, N = 35). After feeding, guans spent 30–60 min ($\bar{x}$ = 47 ± 10 min, N = 35) resting or preening on the fruiting tree. I observed that the same individual would visit the same tree several times during the day. For example, a single *Symplococarpo flavifolium* tree was visited ten times by one male and five times by one female in a single day.

Among cracids, Horned Guans seem typical in their consumption of both fruit and green leaves (Salvin 1860, Salvin and Godman 1902, Wagner 1953, Andrle 1967, Alvarez del Toro 1980). They seem exceptional, however, in that nestlings and fledglings also consume fruit and young

leaves but almost no animal food. Nestlings (N = 4) are fed only fruit and green leaves (González-García, unpubl. data).

Miscellaneous behavior.—I observed Horned Guans sleeping on eight occasions. Three of these observations were done while the birds were perched in feeding trees and five while they were on the nest. Birds rested with their eyes closed and their bills either on their retracted necks or buried within their back feathers. Additionally, yawning (N = 4) was seen at the nest. Each bird stretched its neck and opened its beak wide, similar to a yawn.

Wagner (1953), Leopold (1977), and Estudillo (1979) suggest that Horned Guans are probably among the most terrestrial of the cracids. Contrary to this, I almost always observed Guans in trees of tall or medium height. They descended to the ground only to bathe, court or to ascend slopes. While courting, Guans spent only a few minutes on the ground between flights to trees (González-García, unpubl. data). My observations also conflict with those of Salvin (1860), Wagner (1953), and Alvarez del Toro (1976) who suggested that Horned Guans forage by scratching in leaf litter. I observed Horned Guans foraging or walking on the ground (N = 10) but not scratching in leaf litter. Although I never observed Horned Guans drinking from streams, it is possible that they descend to the ground to do so. However, I observed Horned Guans drinking water accumulated in bromeliads on four occasions.

Horned Guans are poor fliers, as are many cracids. To ascend mountain slopes they use short flights with labored flapping, resembling the flapping flight of the Black Vulture (*Coragyps atratus*) (contra Bubb, in Collar et al. 1992:142). To descend into ravines, they move onto high branches and propel themselves with wings, tail and neck extended. They appear to be extremely agile while gliding through vegetation or when walking or climbing among branches.

Further studies of the Horned Guan would be especially valuable in understanding their ecology and basic biology.

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COMPOSITION AND PHENOLOGY OF AN AVIAN COMMUNITY IN THE RIO GRANDE PLAIN OF TEXAS

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ABSTRACT.—In October–November 1988 and from middle February 1989 through July 1990 we used mist nets to examine the composition and seasonal occurrence of the avifauna in a dry thorn forest community of the north central portion of the Tamaulipan Biotic Province in Texas. Fifty-nine species and 1269 individuals were captured. Many species usually considered to reside permanently in the area were not present from November to March; species considered to be winter residents were caught only in low numbers. During the study, rainfall was 55% and 47% of the annual average. We suggest that the drought conditions were associated with reduction of food resources, forcing birds to abandon the area during the winter of 1989–1990 and to return to breed in low numbers in the spring of 1990. Lack of shrub foliage in spring 1990 may have caused a lower rate of capture for most species in that year because it resulted in the reduction of food resources and shelter. *Received 8 April 1993, accepted 5 Oct. 1993.*

This study provides information about the composition and phenology of an avian community inhabiting the arid thorn forest of the Tamaulipan Biotic Province of Texas. This province, located south of San Antonio between the Rio Grande and the Gulf Coast, is of particular biological interest because it is a region where Neotropical, Sonoran, and Austroriparian species converge (Blair 1950). The dynamics of the region is driven by widely fluctuating rainfall, which causes marked changes in the vegetation (Lehman 1969:140, Norwine and Bingham 1985, Rappole et al. 1986) and indirectly the bird composition (Woodard 1975:47). The most important reference to the avifauna in the central portion of the Tamaulipan Biotic Province of Texas is by Oberholser (1974). However, seasonal distribution here and elsewhere in the region is poorly known for many common species (Rappole 1978, Pulich 1988).

Since the early 1900s, land owners, with the help of the U.S. government, have conducted programs for eradication of thorn forest in a large part of the province to increase forage production for livestock and to make land available for cultivation (Inglis et al. 1986). By 1959, 28% of the region had received some kind of shrub control (Davis and Spicer 1965:7). It is estimated that between 1940 and 1981 about 600,000 ha of thorn forest were treated annually (Welch 1982). These alterations of the vegetation probably have caused large changes in the composition, size, and distribution of the associated avifauna, especially in species depen-

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dent on dense scrub. Unfortunately, baseline data for assessing such changes are lacking. This is the first detailed study of the avifauna of the north central portion of the Tamaulipan Biotic Province. Our objective was to document the avian composition of a thornscrub community and to identify the extent to which the seasonal status of birds in the area corresponds with that reported by other authors.

METHODS AND STUDY AREA

We conducted the study on the 7285-ha T. J. Martin La Campana Ranch (28°02′N, 98°27′W) in McMullen and Duval counties, Texas. Temperatures recorded in Freer, Texas (35 km southwest of the study area) averaged 28°C in the summer and 13°C in the winter, with 125 days >32°C and 17 days <0°C (Natl. Fibers Inf. Cent. 1987). Precipitation data have been collected continuously on the ranch since 1959; rainfall is erratic, both seasonally and annually, and averages 70.5 cm, with peaks in May and September. During the study, rainfall was 55% and 47% of the annual average for 1988 and 1989, respectively, and 69% above the average from January to April 1990. The study area lies 450 m above sea level, and its topography is level to gently rolling. Soils are deep to shallow, and include the Hidalgo, Pettus, and Olmos series (Soil Conserve. Serv. 1985).

Vegetation of the region has been characterized as "Freer mixed brush" (Davis and Spicer 1965:16). In the study area, we sampled vegetation following the technique described by Wiens and Rotenberry (1981). Woody species included 18% blackbrush (*Acacia rigidula*), 15% guajillo (*Acacia berlandieri*), 9% Texas persimmon (*Diospyros texana*), 7% vine ephedra (*Ephedra antisyphilitica*), 6% Texas kidneywood (*Eysenhardtia texana*), 5% blue sage (*Salvia baellatafolia*), 5% Texas colubrina (*Colubrina texensis*), 4% guayacan (*Porlieria angustifolia*), 4% granjeno (*Celtis pallida*), 4% mesquite (*Prosopis glandulosa*), 3% lotebrush (*Condalia obtusifolia*), 3% whitebrush (*Aloysia lycioides*), and 17% other species. Percent shrub coverage and shrub height averaged 55.5 ± 4.2% (± SD) and 1.2 ± 0.6 m (± SD), respectively. The ground between clumps of shrubs was mostly bare, with a few small cacti and other hardy xerophytes, except during the spring of 1991 when grasses and other herbaceous plants covered the ground.

Oil well operations, road construction, and cattle installations were scattered throughout the ranch. The ranch was grazed continuously and cattle ranged freely. Stocking rates varied but averaged 12.5 ha/animal unit.

As a part of an ongoing program at the ranch to improve habitat for white-tailed deer (*Odocoileus virginianus*) and Northern Bobwhites (*Colinus virginianus*) and to investigate the numerical response in bird captures to mechanical clearing of thornscrub strips, three 30–125 ha plots were roller-chopped and three 16–41 ha plots were disced on strips 55–61 m wide alternating with adjacent 244-m wide untreated strips. Roller-chopped and disced strips comprised 20–29% of each section, respectively. Four sites, 1–3 km apart, were selected to sample birds: Sites 1 and 2 each consisted of a disced strip and an adjacent untreated scrub. Sites 3 and 4 consisted of a roller-chopped strip and adjacent untreated scrub. Woody species composition on the treated strips was similar to that in the adjacent untreated scrub, but shrub cover was reduced by 89–98% and remained low and short (20–50 cm) during the 1.5 years of the study (Bozzo et al. 1992).

Forty mist nets (4 shelves, 12 × 2.6 m, 36-mm mesh) were placed in sets of 10 on the four study sites. At each site, nets were deployed at 50-m intervals: five along a line in the center of the treated strips and five 50 m from the border in the adjacent scrub. Net locations were the same throughout the study.

We mist-netted birds in October–November 1988 from middle February 1989 through July 1990, yielding a total of 22,323 net-h. Numbers of net-h by season were 3948 (1989) and 4399 (1990) during the spring (Mar.–May); 5142 (1989) and 520 (1990) in the summer (Jun.—Aug.); 684 (1988) and 4207 (1989) in the fall (Sept.–Nov.); and 3493 in the winter of 1989–1990 (Dec.–Feb.).

We sampled birds for two consecutive days in two-week cycles: week 1, sites 1 and 2; week 2, sites 3 and 4; consequently, for each capture site the birds were not subjected to netting for 13 days after the two-day sampling period. We maintained this schedule to minimize net shyness. We netted from dawn to dusk, except in summer, when we closed the nets during the hottest hours of the day.

Each bird captured was banded with a U.S.F.W.S. aluminum band and examined to determine sex and age (when possible). Date, time, site, and net of capture were also recorded.

RESULTS

We captured 1269 individuals of 59 species during the study (common and scientific names are provided in Figs. and Appendix I). Seven species made up 68% of total captures. They were, in order of decreasing abundances, Pyrrhuloxia, Common Ground-Dove, Northern Mockingbird, Painted Bunting, Cassin's Sparrow, Black-throated Sparrow, and White-crowned Sparrow. Ten additional species comprised 20% of the captures. Arranged in decreasing abundance these were Curve-billed Thrasher, Olive Sparrow, Northern Oriole, Northern Cardinal, White-eyed Vireo, Long-billed Thrasher, Scissor-tailed Flycatcher, Lark Sparrow, Cactus Wren, and Brown-headed Cowbird. The remaining 47 species accounted for only 12% of the sample.

In showing data on seasonal occurrence, the species are divided into (1) permanent residents—present throughout the year, (2) summer residents—present and breeding only in the summer months, (3) winter residents—present through the winter months, and (4) transients—present only during migration.

Permanent residents.—This group was represented by 950 individuals from 17 species considered to be present throughout the year in the Coastal Bend (Rappole and Blacklock 1985), lower Rio Grande Valley (Griscom and Crosby 1925, 1926; Oberholser 1974), and the remainder of the Tamaulipan Biotic Province of Texas (Oberholser 1974). The bulk of captures occurred from early March to early November (Fig. 1). For all of these species, the combined rate of capture (birds/net-h) remained fairly constant during the spring (0.05), summer (0.06), and fall (0.03), but declined sharply during the winter (0.007). The Verdin, Cactus Wren, Northern Cardinal, Cassin's Sparrow, Lark Sparrow, Brown-headed Cowbird, and Bronzed Cowbird were not caught at all during the winter.

Considering only AHY-birds (N = 604), the sample was composed of 329 males, 212 females, and 63 birds of unknown sex. Segregation of

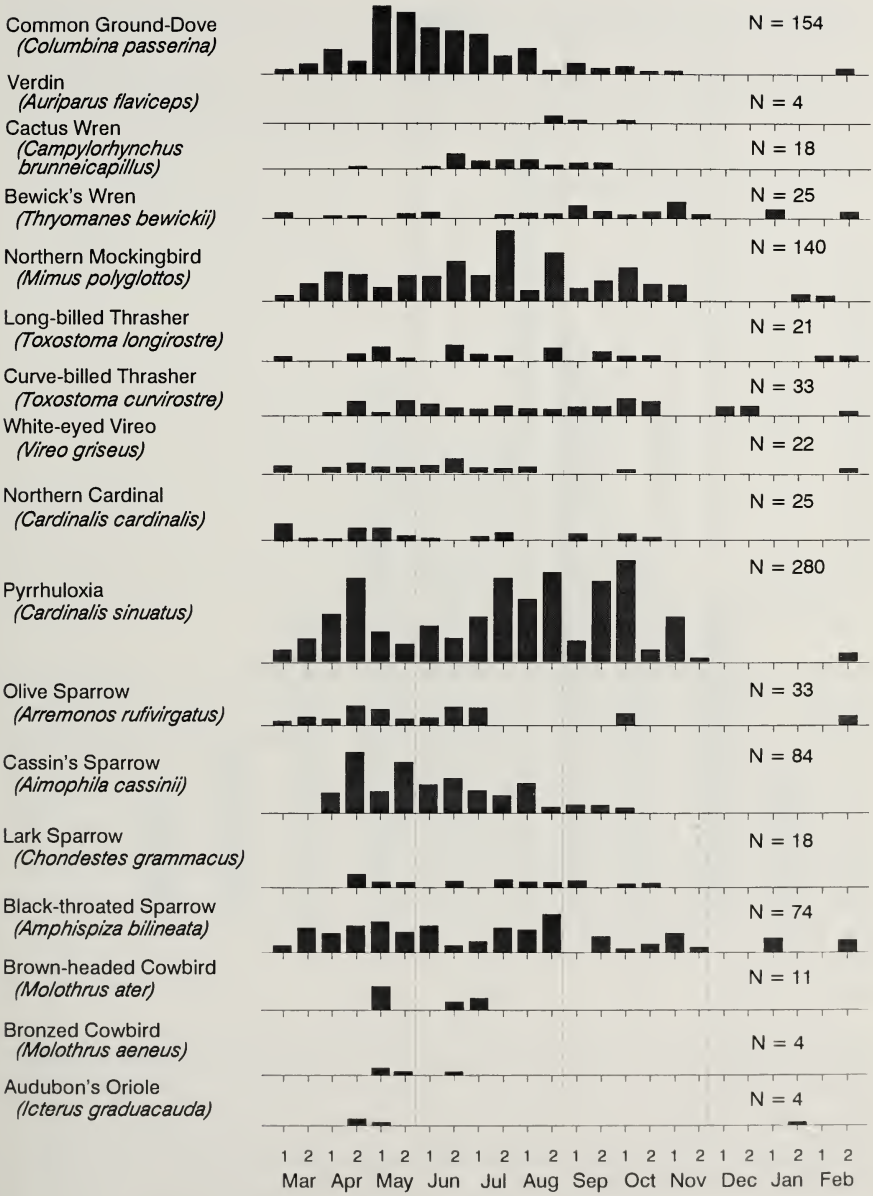

FIG. 1. Distribution of species considered permanent residents (Oberholser 1974); bars represent proportional occurrence at two week intervals.

TABLE 1

MONTHLY PERCENTAGE DISTRIBUTION OF AGE AND SEX CLASS FOR BIRDS CLASSED AS "PERMANENT" AND "SUMMER" RESIDENTS, LA CAMPANA RANCH, MCMULLEN AND DUVAL COUNTIES, TEXAS, 1988–1990 (SEE TEXT FOR EXPLANATION)

	Permanent residents								Summer residents							
		Sex[a] (%)				Age (%)				Sex[a] (%)				Age (%)		
Month	N	M	F	U	N	AHY	HY	U	N	M	F	U	N	AHY	HY	U
Jan	4	25	0	75	5	100	0	0	—	—	—	—	—	—	—	—
Feb	17	35	12	53	17	100	0	0	—	—	—	—	—	—	—	—
Mar	52	43	29	28	52	100	0	0	—	—	—	—	—	—	—	—
Apr	171	57	32	12	171	100	0	0	12	75	0	25	12	100	0	0
May	172	62	37	1	186	92	7	1	62	60	28	12	64	97	2	1
Jun	109	56	40	4	145	75	23	2	21	41	50	9	27	79	21	0
Jul	50	46	48	6	125	40	60	0	25	20	44	36	42	60	40	0
Aug	15	20	33	47	90	17	74	9	3	67	0	33	15	20	80	0
Sep	2	100	0	0	40	5	70	25	2	50	0	50	6	33	17	50
Oct	8	50	38	12	90	9	57	34	1	100	0	0	3	33	0	67
Nov	4	75	0	25	29	14	24	62	—	—	—	—	—	—	—	—

[a] Considering only AHY-birds.

monthly captures by sex indicates that males were more often caught than females except for July and August, when the relationship was reversed (Table 1). Small samples from September to January and proportionally large captures of birds of unknown sex in February, March, and August may bias this presumed relationship. The difference in numbers of males captured versus number of females, however, was substantial for the Common Ground-Dove (73M, 49F, 5U), Curve-billed Thrasher (15M, 3F, 3U), Olive Sparrow (21M, 2F, 4U), Cassin's Sparrow (36M, 15F, 7U), and Black-throated Sparrow (23M, 8F, 13U). Nearly even sex ratios occurred in the Northern Mockingbird (34M, 36F, 11U) and Pyrrhuloxia (73M, 63F, 6U).

Our sample included 316 birds in breeding condition (i.e., birds with cloacal protuberance and/or incubation patch) representing all of the permanent resident species except the Verdin. Individuals in breeding condition were present from early March to early August, with the peak occurring from late April to early July (Figs. 2 and 3). We were unable to determine breeding status for the Common Ground-Dove, Brown-headed Cowbird, and Bronzed Cowbird.

Capture of HY-birds started in early May. After late July more HY-birds than AHY-birds were captured, with a peak in HY captures from July to August (Table 1). Occurrence and number of HY-birds captured varied among species.

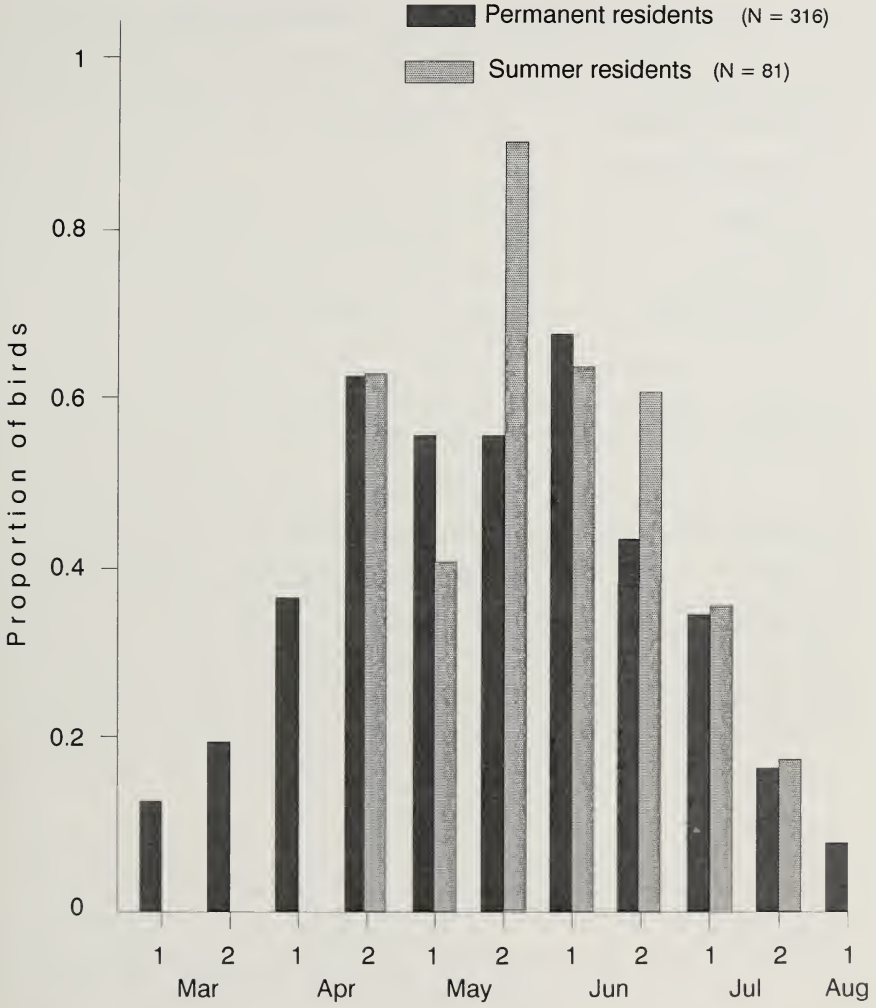

FIG. 2. Biweekly proportion of birds in breeding condition for permanent and summer resident species.

Summer residents.—This group was represented by 169 individuals of 10 species considered to be present and breeding only in the summer months in Coastal Bend (Rappole and Blacklock 1985), lower Rio Grande Valley (Griscom and Crosby 1925, 1926; Oberholser 1974), and remainder of the Tamaulipan Biotic Province of Texas (Oberholser 1974). Most individuals of these species arrived by late April and departed by late August (Fig. 4). For all species combined, capture rates (birds/net-h) re-

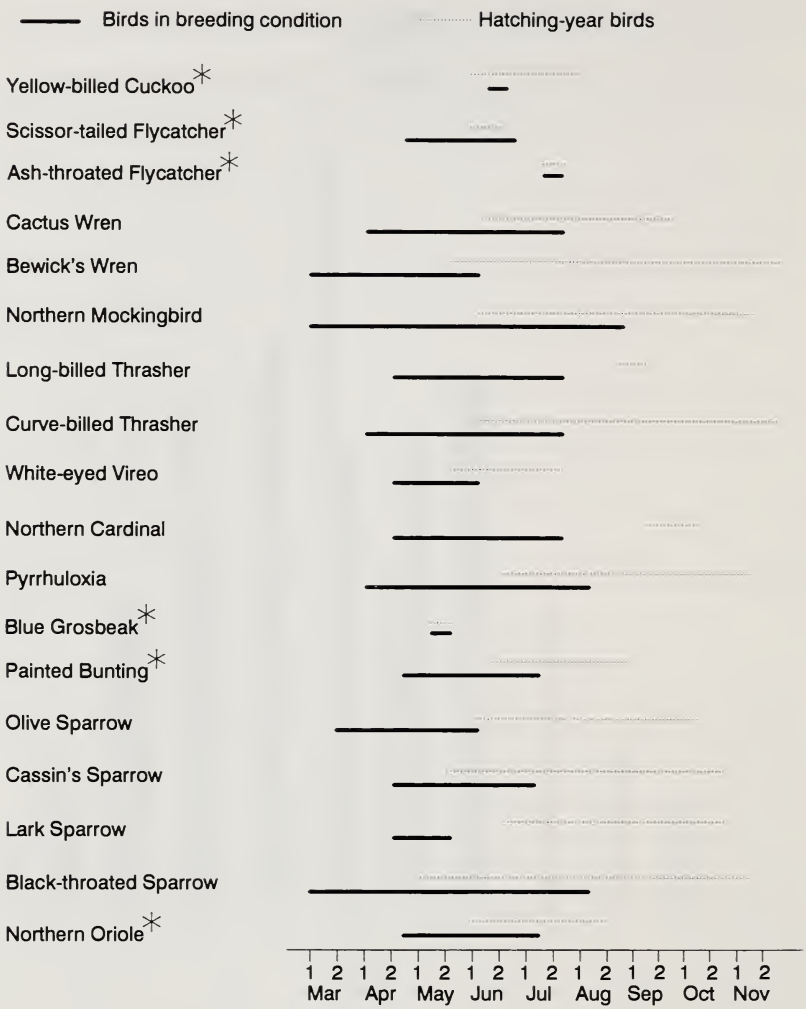

FIG. 3. Presence of individual species and hatching-year birds of permanent and summer (*) resident species.

mained fairly constant during the spring (0.010) and summer (0.015) and declined in the fall (0.002). Considering only AHY-birds (N = 126), the sample was composed of 64 males, 38 females, and 24 birds of unknown sex. Segregation of monthly captures by sex and age is presented in Table 1. Twelve birds of these species were recaptured, but only one individual was recaptured between years, a Painted Bunting (28 Apr. 1989 and 11 Apr. 1990). Our sample included 81 birds in breeding status. The Brown-

crested Flycatcher and Bell's Vireo are supposed to be "summer residents" in this region, but they occurred in low numbers, and none was captured in breeding condition. Summer residents in breeding condition were present from late April to late July, with a peak in late May (Figs. 2 and 3).

Winter residents.—This group was represented by 91 individuals of 13 species considered to be present only during the winter months in the Coastal Bend (Rappole and Blacklock 1985), lower Rio Grande Valley (Griscom and Crosby 1925, 1926; Oberholser 1974), and remainder of the Tamaulipan Biotic Province of Texas (Oberholser 1974). However, our data indicate that rather than winter residents, these birds were probably transients. Although these species were present from early September to early May, only seven individuals of five species were caught from December to February (Fig. 5). The sample was dominated by AHY-birds and un-sexed birds.

Transients.—This group was represented by 59 individuals of 19 species considered to occur only during migration in the Coastal Bend (Rappole and Blacklock 1985), lower Rio Grande Valley (Griscom and Crosby 1925, 1926; Oberholser 1974), and remainder of the Tamaulipan Biotic Province of Texas (Oberholser 1974) (Appendix I). They were present in the area from late March to late May in spring and from early September to late October in fall. Peaks in numbers of species and individuals caught occurred in early May and early October. Spring and fall samples were composed of 15 and 11 species, respectively.

DISCUSSION

Categorization of the status of bird species in this area is uncertain. "Permanent residents" are defined as those species that reside in the same area throughout the year (Pulich 1988). However, species listed as permanent residents in our study area (Oberholser 1974) were not present in the winter of 1989–1990. Even though we saw a few individuals of some of these species, it was evident that the majority were gone by late October and did not return until late April. Clearly, many species that are considered to be resident and nonmigratory show seasonal movements. The assumed seasonal status for most of these species in the central portions of the Tamaulipan Biotic Province of Texas is an extrapolation from what we know of populations in the Coastal Bend and Lower Rio Grande Valley. But our data indicate that this information may not apply for some species that inhabit the drier and climatically more extreme central area of this province.

Where these species go during the winter is uncertain, but there is some evidence that inland populations move toward the coast. The Long-billed

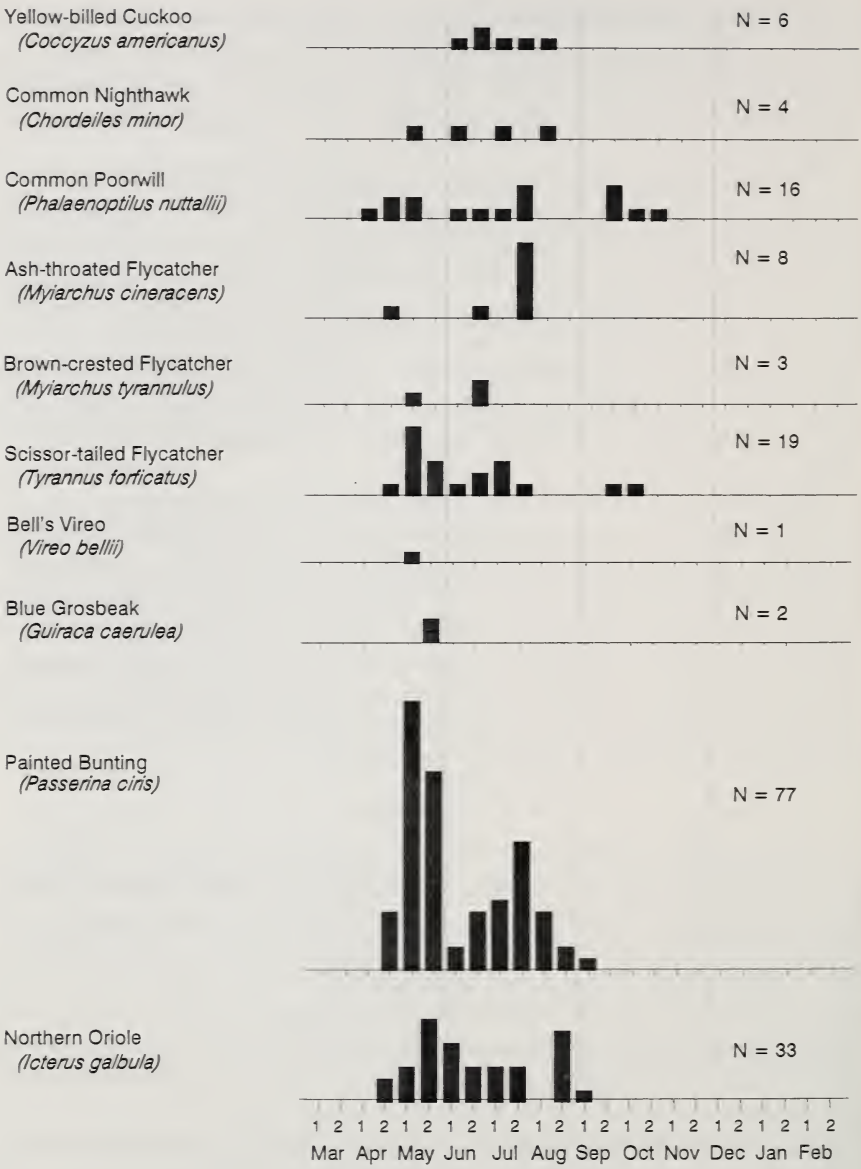

FIG. 4. Distribution of species considered "summer residents" (Oberholser 1974); bars represent proportional occurrence at two week intervals.

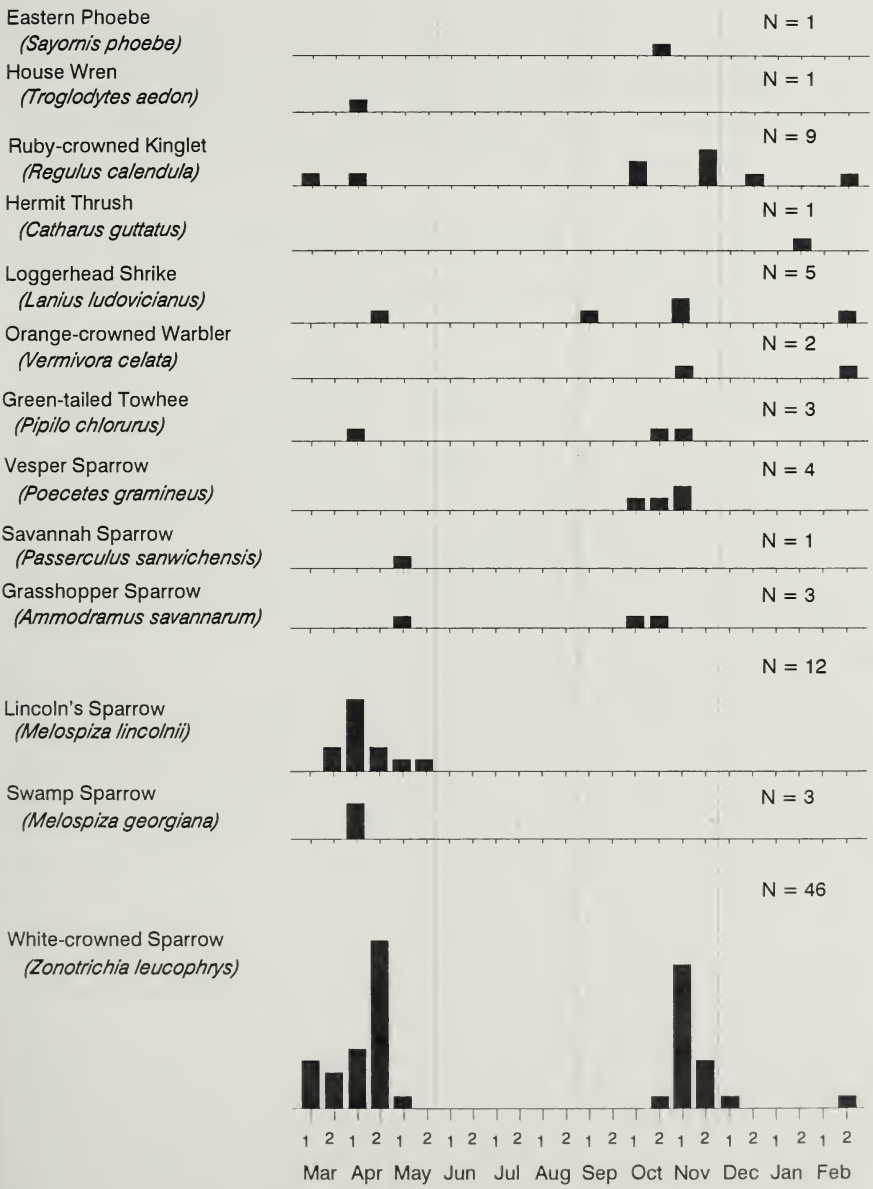

FIG. 5. Distribution of species considered "winter residents" (Oberholser 1974); bars represent proportional occurrence at two week intervals.

Thrasher, Northern Cardinal, Pyrrhuloxia, and Brown-headed Cowbird are more numerous along the immediate coast during the winter (Rappole and Blacklock 1985); the Black-throated Sparrow has been reported only in December at the Aransas National Wildlife Refuge (USFWS 1980), which is on the coast, and from December to March for the central coast (Hagar and Packard 1952).

These movements may reflect responses to changes in climatic conditions (Terrill and Ohmart 1984, Petit 1989). Our data show that not only species considered to be permanent residents on the study area were mostly gone during the winter but also that species that were expected to be winter residents were captured in low numbers. Of 91 individuals of "winter resident" species only seven were caught from December to February; the remaining 84 individuals were apparently transients. Griscom (1920, in Bent 1968:991) reported that the Black-throated Sparrow disappeared from the vicinity of San Antonio with the first cold weather. In our study area temperatures in the winter of 1989–1990 ranged from 0°C to 15°C in January and early February; however, low temperatures, especially during the nights and mornings, occurred from late November to late February. Freezing temperatures occurred from 14 to 17 December and again on 23 and 24 December.

Availability of food may play a role in these movements (Graber and Graber 1979, Van Balen 1980). For our study area, 1988 and 1989 were dry years; rainfall recorded at the ranch was only 55% and 47% of the annual average, respectively. In the winter of 1989–1990, the scrub vegetation was so dry and reduced by the falling or withering of leaves that the supply of food at this time may have declined to a level that made the area unsuitable for insectivorous foliage gleaning species such as the Verdin and White-eyed Vireo which were not seen at all. Several granivorous species such as the Common Ground-Dove, Northern Cardinal, and Pyrrhuloxia which were not caught or seen on our study plots were, however, seen close to the main camp where there were seeds on the roads. Oberholser (1974:702) mentioned that the White-eyed Vireo winters in the region in areas where shrubs keep their leaves through the winter; Henshaw (in Bent 1948:230) reported that during the winter in California, the Cactus Wren moved for days or weeks to areas with denser cover.

Movements over much longer distances may occur as well. Rappole et al. (in press) recently summarized information on presence of regular migration movements into the Neotropics by species presumed to be permanent residents in the Tamaulipan Biotic Province. Most of these species were large, conspicuous daytime migrants in which actual migration flights could be observed on the Veracruz coast (e.g., Great Black Hawk

[*Buteogallus urubitinga*] and Short-tailed Hawk [*Buteo brachyurus*]). Detection of such movements may require extensive banding studies.

Comparison of captures between the springs of 1989 and 1990, which had similar netting efforts revealed important changes in both composition and abundance of bird species. More individuals were captured in 1989 than in 1990 (N_{1989} = 353, N_{1990} = 132; *G*-test of goodness of fit, G = 104.5, df = 1, $P < 0.001$). At the species level, all species were caught in larger numbers in 1989 than 1990. The Brown-crested Flycatcher, Verdin, Cactus Wren, Long-billed Thrasher, Curve-billed Thrasher, White-eyed Vireo, Bell Vireo, and Olive Sparrow were captured in 1989 but not in 1990.

Lack of foliage in most shrubs in the spring of 1990 probably played a major role in the large decline in capture rates of breeding individuals from 1989 to 1990 (N_{1989} = 353, N_{1990} = 132; *t*-test for paired comparisons, T = 4.24, $P < 0.001$), because it resulted in the reduction of food resources and shelter. In 1989, shrubs had foliage at least until the end of the breeding season. A continuing shortage of rain and the occurrence of freezing temperatures in December left most shrubs without leaves. In the spring of 1990, as a result of the rainfall, a lush growth of forbs and grasses covered most of the ground; however, most shrubs, particularly blackbrush, were still essentially leafless by June. This lack of shrub foliage may have caused the low numbers of captures for those species that depend on shrubs for nesting (14 in our study area). Of the few species of shrubs that kept their leaves, guajillo was the most common; however, because of the windy environment of the study area, the extreme flexibility of its branches made it inappropriate for nest placement. Species such as the Cassin's and Black-throated Sparrows, that often nest on the ground, were captured in similar numbers in the springs of both years.

Heavy growth of forbs and grasses made the habitat suitable for species primarily associated with weedy and grassy fields, such as Savannah, Grasshopper, Lincoln's, and Swamp sparrows, which were caught in the spring of 1990 but not in 1989. However, this situation may have contributed to the low capture rate of other species that need bare ground for feeding. Roth (1971) mentioned that the dense, tall herb cover probably caused the absence of the Common Ground-Dove, Northern Mockingbird, Long-billed Thrasher, Curve-billed Thrasher, and Northern Cardinal in some of his study sites.

In a rapidly fluctuating environment, e.g., the Tamaulipan Biotic Province of Texas, birds must be able to choose breeding and wintering sites according to local conditions. The idea of birds moving to other areas during the winter and changing location for breeding when the habitat is not suitable is possible but unproven.

We consider that birds inhabiting the central portion of this province are subjected to more extreme and variable climatic conditions than those inhabiting the Coastal Bend and Lower Rio Grande Valley. Periodic climatic extremes apparently constitute a primary force that determines the composition and abundance of the birds, as has been suggested for birds inhabiting grassland-shrubsteppe communities (Wiens 1974, Knopf et al. 1990, Zimmerman 1992). In wet years, when the rainfall is sufficient to bring the scrub and mesquite trees into complete green leaf and the winters are not harsh, the area may be populated by species that extend their breeding distribution, winter residence, or stopovers during migration. In dry years, however, the bird community is quite reduced. Roth (1979, p. 168) alluded to this pattern for Dickcissels (*Spiza americana*) which, ". . . nest in South Texas in wet years when the grass is lush but pass by in dry years without nesting." He added that this behavior may, ". . . represent past selection on a northern population to breed earlier or to raise an extra brood, or selection on a southern population to compensate for unpredictable weather and vegetation conditions by moving north when conditions become poor." We suggest that facultative movements of this nature may be the rule among birds using the central portion of the Tamaulipan Biotic Province of Texas.

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Appendix I

Total Number of Individuals of Transient Species Captured at La Campana Ranch, McMullen and Duval Counties, Texas, 1988–1990

Yellow-bellied Flycatcher (*Empidonax flaviventris*), 3
Acadian Flycatcher (*E. virescens*), 2
Alder-Willow Flycatchers (*E. traillii-alnorum*), 8
Least Flycatcher (*E. minimus*), 1
Eastern Phoebe (*Sayornis phoebe*), 1
Great Crested Flycatcher (*Myiarchus crinitus*), 1
Blue-gray Gnatcatcher (*Polioptila caerulea*), 16
Swainson's Thrush (*Catharus ustulatus*), 1
Solitary Vireo (*Vireo solitarius*), 1
Blue-winged Warbler (*Vermivora pinus*), 1
Nashville Warbler (*V. ruficapilla*), 5
Magnolia Warbler (*Dendroica magnolia*), 4
Black-throated Green Warbler (*D. virens*), 3
Bay-breasted Warbler (*D. castanea*), 1
American Redstart (*Setophaga ruticilla*), 1
Mourning Warbler (*Oporornis philadelphia*), 2
Wilson's Warbler (*Wilsonia pusilla*), 4
Yellow-breasted Chat (*Icteria virens*), 2
Indigo Bunting (*Passerina cyanea*), 2

Wilson Bull., 106(2), 1994, pp. 381–390

UNDERSTORY AVIFAUNA OF A BORNEAN PEAT SWAMP FOREST: IS IT DEPAUPERATE?

James C. Gaither, Jr.[1]

Abstract.—Southeast Asian peat swamp forests support fewer birds than dipterocarp forest. Habitat preferences appear to exist; seven species were captured significantly more often in the dipterocarp forest, and two species were represented by significantly more captures in the peat swamp forest. An increase in number of frugivorous birds in the peat swamp forest in June was correlated with a large fruit crop of *Callocarpa* sp. The difference in abundance of understory birds between the peat swamp forest and the dipterocarp forest resulted largely from three insectivorous guilds. Rare species constituted a large portion of captures, and a single family of insectivores (Timaliidae) were particularly rich in number of individuals and number of species. Peat swamp forests, although they may support a reduced understory avifauna relative to lowland dipterocarp forest, appear important in the ecology of Southeast Asian avian communities because they support specialized species and attract frugivores at sporadic intervals. *Received 4 May 1993, accepted 2 Nov. 1993.*

Our knowledge of Southeast Asian bird communities is based primarily on research conducted in pristine and regenerating lowland dipterocarp forest (Fogden 1972, Pearson 1977, Karr 1980, Wong 1986). The avifaunas of other forest formations, such as freshwater swamp forest, heath forest, mangrove forest, montane forest, and peat swamp forest (Whitmore 1984), remain largely unexplored. The avifauna of peat swamp forests is particularly worthy of investigation because such forests are widespread in Southeast Asia and are thought to support a depauperate animal community. Peat swamp forests cover 14,660 km^2 (12% of the total land area) of Sarawak, Malaysia, and in Brunei, peat swamp forests occupy 980 km^2 (23% of the total land area) (Anderson 1964). Peat swamp forests are thought to support depauperate animal communities because of the cascading influence of poor soil characteristics (Janzen 1974). The soils of peat swamp forests are rich in organic matter, acidic ($pH \leq 4.0$), deficient in mineral nutrients, and often water-logged (Whitmore 1984:180). Janzen (1974) suggested these poor soil characteristics are responsible for structurally simplistic, slow growing, and chemically well-defended vegetation. Under this line of reasoning, plant biomass production is extremely limited and most of what is produced is toxic, creating a dramatic limitation to the productivity of higher trophic levels including birds.

I used mist nets to compare the understory bird community in a peat swamp forest with the understory bird community of an adjacent lowland

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dipterocarp forest growing on the fertile soils of an alluvial terrace in Borneo. Here, I examine the composition and dynamics of foraging guilds and test the predictions that (1) the number of individual understory birds is lower in the peat swamp forest than the dipterocarp forest within the area of study and (2) the number of species of understory birds is lower in the peat swamp forest than the dipterocarp forest within the area of study.

STUDY AREA AND METHODS

I conducted this research in the Cabang Panti Research Site in the Gunung Palung Nature Reserve (now National Park) (1°13′S, 110°7′E) in West Kalimantan (Borneo), Indonesia. The study area lies just above sea level and contains a 17-ha tract of peat swamp forest adjacent to a 48-ha tract of lowland dipterocarp forest on alluvial terrace. The study area is bounded on the north by extensive dipterocarp forest on the slopes of Mount Palung (1160 m), and on the south by peat swamp forest and freshwater swamp forest on a broad coastal plain.

Total rainfall was 4715 mm during the year in which this research took place, August 1986 to July 1987. The driest month was August with only 11 mm. February, June, and July were relatively dry with 120 mm, 275 mm, and 118 mm of rain, respectively. All other months were very wet with rainfall from 371 mm to 669 mm per month. Temperature records are unavailable, but no extremes were noted.

Vegetation structure of lowland dipterocarp forest and peat swamp forest differ greatly. The dipterocarp forest in which this study took place, is the classic, cathedral-like Southeast Asian tropical lowland evergreen rain forest, which is dominated by trees in the Dipterocarpaceae. Emergent trees exceed 60 m in height over a multi-layered and dense canopy. Mean diameter of trees is very large, with many trees exceeding 2 m in diameter. Lianas, epiphytes, and hemiepiphytes are abundant in the canopy. Compared to the dipterocarp forest, the peat swamp forest structure is stunted and sparse. Emergent trees, where present, reach heights of 20–30 m over a single-layer canopy. Mean size of trees is small; few trees exceed 0.5 m in diameter. The canopy is thin and supports relatively few lianas, epiphytes, and hemiepiphytes. Brunig (1983), Anderson (1964, 1983), and Whitmore (1984) provide more information on vegetation.

From December 1986 to July 1987, I operated ten mist nets (12 m long, 2.6 m high, 36 mm mesh, 4 shelf) at ground level for two days per month in each habitat. Mist nets are widely used in studies of tropical understory bird communities (Karr 1980, Schemske and Brokaw 1981, Wong 1986, Levey 1988, Loiselle and Blake 1991). I did not sample both habitats simultaneously; I netted for two days in one habitat, spent one day moving the nets, and then netted for two days in the other habitat. I opened the nets at dawn (06:30) and closed them after a minimum of 10 h (16:30–18:00) unless rain forced an early closure. Rain forced early net closing five times in the dipterocarp forest and three times in the peat swamp forest. In all cases, the rain fell after 14:00. There was very little variation in weather conditions between netting days in the two habitats. I accumulated 1509 net-h in the peat swamp forest and 1512 net-h in the dipterocarp forest (1 net-h = 1 mist net open for one hour).

There were 20 mist-net sites in each habitat. I used ten sites one month and the other ten sites the next month. Each mist-net site was randomly placed along a pre-existing trail system with 10 m to 50 m distance between each site. Twenty sites were used in each habitat, as opposed to just ten, to maximize the number of different patch types sampled.

Patch types range from recent tree fall gaps to mature canopy, and it is possible that as a patch of forest changes through time, the bird assemblage that utilizes the patch may also change (Schemske and Brokaw 1981). I strove to maximize the number of different patches in which I placed mist nets, so as to increase my chances of sampling all bird species present in each forest habitat.

I identified each captured bird following the nomenclature of King et al. (1975), and I released all birds at the capture location. I assigned each species to one of ten foraging guilds, using the guild classifications of Wong (1986). For some analyses, I lumped foraging guilds into guild categories of insectivore, frugivore, and nectarivore. The sample size determined the appropriate statistical test. If $N > 200$, I used Chi-square, if $200 \geq N \geq 25$ I used Chi-square adjusted for small sample sizes, and if $N < 25$ I calculated the expected binomial probabilities (Sokal and Rohlf 1981:708). I used the Wilcoxon signed-ranks test to evaluate some data on a month by month basis.

Because numbers of birds increased in the peat swamp forest in June, I conducted fruit tree watches, and I censused the standing fruit crop in both habitats during the same week in which I mist netted. Fruit tree watches consisted of standing at a distance of 10 to 20 m from *Callocarpa* sp. (Verbenaceae) trees and observing all bird feeding activity with binoculars (10 × 40). I kept a tally for all bird species observed and of all instances in which I observed a bird swallowing a fruit. I accumulated 5.2 h of observation over five consecutive mornings between 06:30 and 09:30. These observations were not incorporated into the mist net capture record. The fruit crop census consisted of quantifying the fruit crop available in both habitats in June. I searched two 20 m × 250 m randomly chosen transects in each habitat for any plants (including lianas and epiphytes) bearing ripe fruit. Where fruit was present, I determined the species of plant if possible and estimated the size of the fruit crop.

RESULTS

The data support the first prediction that the number of individual understory birds should be lower in the less productive peat swamp forest than in the dipterocarp forest sampled in this study. The total number of individuals captured in the peat swamp forest (230) was significantly lower than in the dipterocarp forest (301) ($\chi^2 = 9.49$, $P = 0.002$). The data do not support the second prediction that the number of species of understory birds should be lower in the peat swamp forest than the dipterocarp forest. There was no significant difference between the total number of species in the peat swamp forest (34) and the dipterocarp forest (39) ($\chi^2_{adj} = 0.21$, $P = 0.558$).

There was a strong tendency towards fewer individuals and fewer species in the peat swamp forest on a month by month basis (Fig. 1). In all months except June, I captured fewer individuals in the peat swamp forest than in the dipterocarp forest (Wilcoxon signed-ranks test, $T_s = 6$, $P = 0.0547$). In all months except June and July, I captured fewer species in the peat swamp forest than in the dipterocarp forest (Wilcoxon signed-ranks test, $T_s = 6$, $P = 0.0547$).

The data suggest that habitat preferences do exist among the understory birds sampled in this study. To determine whether there were significant between-habitat differences in capture frequency for any given species, a

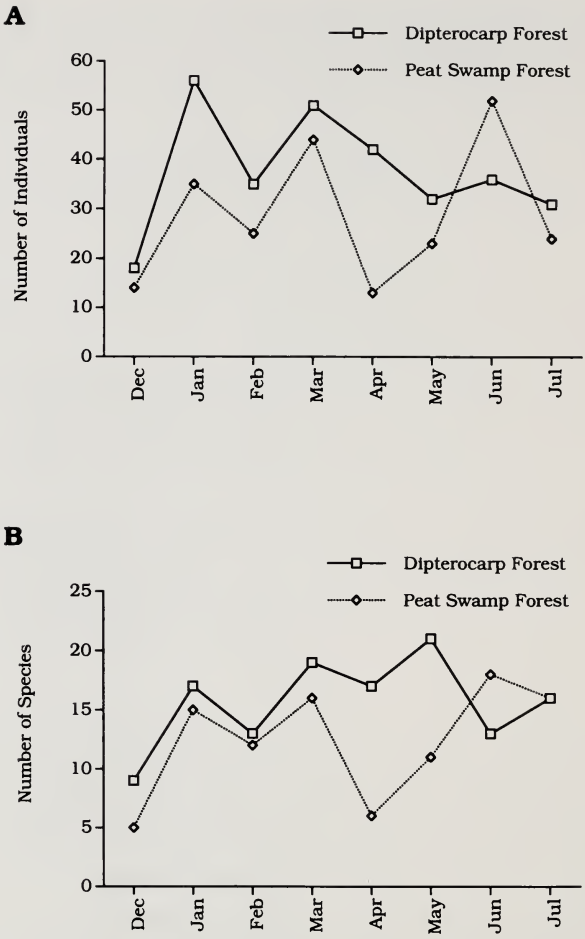

FIG. 1. Number of individual understory birds (A) and number of species of understory birds (B) captured per month in the dipterocarp forest and the peat swamp forest.

minimum of six captures is required to attain the 5% level of significance. Of the 47 species captured in this study (species list and data set available on request from JCG), 22 fulfill this criterion. Based on random processes, we expect 5% of the 22 species (=1.1) to show a significant difference in capture frequency between the two habitats. Of the 22 species, nine showed significant differences in capture frequency at the 0.05 level (Table 1), suggesting that the assemblage of understory bird species that occupied the peat swamp forest was distinct from the assemblage in the dipterocarp forest.

TABLE 1
SPECIES WITH SIGNIFICANT BETWEEN-HABITAT DIFFERENCES IN CAPTURE FREQUENCY[a]

	Number of individuals			Guild type[b]
	PSF	DF	*P*	
White-rumped Shama (*Copsychus malabaricus*)	3	10	=0.035	SFGI
Yellow-bellied Bulbul (*Criniger phaeocephalus*)	15	37	<0.005	I/F
Hairy-backed Bulbul (*Hypsipetes criniger*)	1	7	=0.031	I/F
Gray-breasted Babbler (*Malacopteron albogulare*)	14	1	<0.001	SFGI
Scaly-crowned Babbler (*M. cinereum*)	20	46	<0.005	TFGI
Buff-necked Woodpecker (*Meiglyptes tukki*)	0	6	=0.016	BGI
Yellow-breasted Flowerpecker (*Prionochilus maculatus*)	25	11	<0.05	I/F
Ferruginous Babbler (*Trichastoma bicolor*)	0	8	=0.004	TFGI
Short-tailed Babbler (*Malacocinela malaccensis*)	3	23	<0.001	LGI

[a] PSF = peat swamp forest; DF = dipterocarp forest.
[b] See Table 2 for guild codes.

The only month in which I recorded more individuals and more species in the peat swamp forest than in the dipterocarp forest was June (Fig. 1). The increased number of understory birds in the peat swamp forest in June consisted primarily of insectivore-frugivores, which are in the frugivore guild group (Fig. 2). The number of individual insectivore-frugivores captured in the peat swamp forest in June (25) significantly exceeded the number of insectivore-frugivores captured in the dipterocarp forest in June (7) ($\chi^2_{adj} = 9.03$, $P < 0.005$). The insectivore-frugivore guild is dominated by bulbuls (Pycnonotidae). In the peat swamp, the mean number of individual bulbuls captured in each of the previous six months was 2.3, whereas in June 1987 I captured 19 individual bulbuls and added two new bulbul species to the capture record.

In June in the peat swamp forest, I noticed mixed species flocks, predominantly bulbuls, feeding on the fruit of a single tree species, thought to be in the genus *Callocarpa* (Verbenaceae). During fruit tree watches of *Callocarpa* sp. trees, I recorded 132 observations of insectivore-frugivores and arboreal frugivores eating *Callocarpa* sp. fruit; 78% of those observations were of bulbuls.

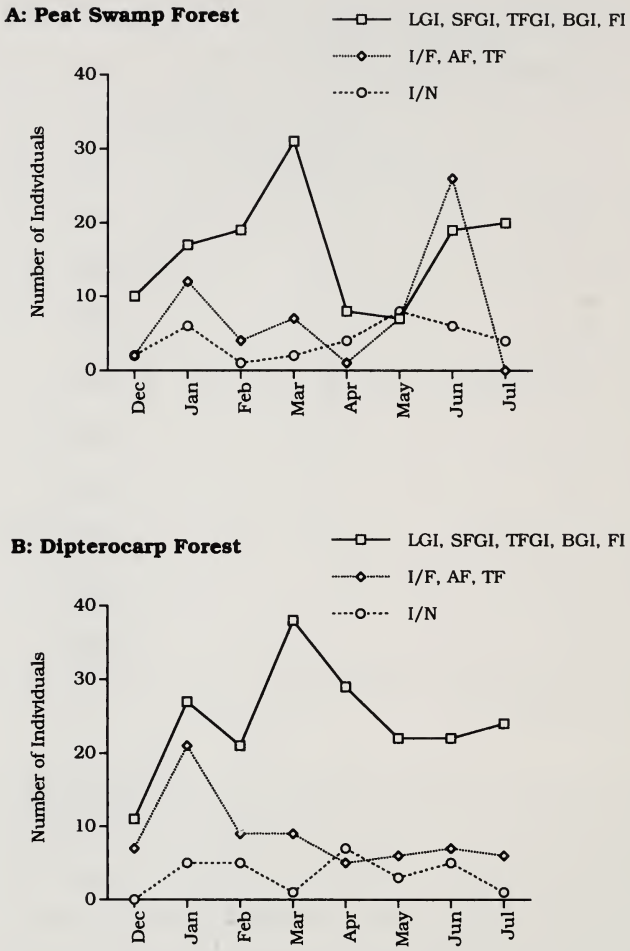

FIG. 2. Monthly captures of understory birds by guild groupings, insectivore (LGI, SFGI, TFGI, BGI, FI), frugivore (I/F, AF, TF), and nectarivore (I/N) in the peat swamp forest (A) and the dipterocarp forest (B). Guild abbreviations are defined in Table 2. Note the peak of frugivore abundance in June in the peat swamp forest.

Fruit was more abundant in the peat swamp forest in June. Within the peat swamp forest transects, I found 18 *Callocarpa* sp. trees each with abundant quantities of ripe fruit (estimated mean crop size of 2500 fruits) and one *Medinilla* sp. (Melastomataceae) epiphyte bearing 5–10 ripe fruits. Within the dipterocarp forest transects, I found one unidentified liana bearing 40–60 ripe fruits and two *Pternandra* sp. (Melastomataceae) trees each with 20–30 ripe fruits.

TABLE 2

DISTRIBUTION BY GUILD OF ALL BIRDS CAPTURED IN THE UNDERSTORY. PROBABILITY VALUES ARE LISTED FOR COMPARISONS OF NUMBER OF INDIVIDUALS BETWEEN HABITATS[a]

Guild type	Number of individuals			Number of species	
	PSF	DF	*P*	PSF	DF
Litter-gleaning insectivore (LGI)	13	37	<0.005	4	3
Shrub foliage-gleaning insectivore (SFGI)	31	28	<0.9	7	8
Tree foliage-gleaning insectivore (TFGI)	54	83	<0.025	5	5
Bark-gleaning insectivore (BGI)	3	12	=0.013	2	4
Flycatching insectivore (FI)	30	34	<0.9	3	3
Insectivore-nectarivore (I/N)	33	27	<0.9	3	2
Insectivore-frugivore (I/F)	58	68	<0.5	8	8
Arboreal frugivore (AF)	1	1	=0.5	1	1
Terrestrial frugivore (TF)	0	1	=0.5	0	1
Miscellaneous (Misc)	7	10	=0.148	1	14
Total	230	301		34	39

[a] PSF = peat swamp forest, DF = dipterocarp forest.

DISCUSSION

The reduced number of individuals, and the trend towards fewer species of understory birds in the peat swamp forest relative to the dipterocarp forest, is consistent with the hypothesis that peat swamp forests support a depauperate animal community (Janzen 1974). More research is required to understand the mechanisms responsible, particularly the possible connection between soils, vegetation, and fauna hypothesized by Janzen. A productive avenue of future study might be to study insectivorous birds because the difference in total number of captures between the peat swamp forest and dipterocarp forest consisted primarily of insectivores. Of nine guilds represented by captures in both habitats, only three guilds showed significant differences in total number of captures, and they were all insectivore guilds. Litter-gleaning insectivores, tree foliage-gleaning insectivores, and bark-gleaning insectivores were caught in significantly lower numbers in the peat swamp forest than in the dipterocarp forest (Table 2).

The general composition of the understory bird community sampled in this study is consistent with that of a virgin lowland dipterocarp forest in the Pasoh Forest Reserve, Peninsular Malaysia (Wong 1986). Rare species, defined as species whose cumulative number of individual captures is less than 2% of the total number of individual captures for all species (Karr 1971), constituted 62% of the species netted in the peat swamp

TABLE 3
SPECIES TABULATED BY THEIR NUMBER OF CAPTURES[a]

Species represented by	Number of species	
	PSF	DF
>21 Captures	3	5
10–20 Captures	5	2
2–10 Captures	16	17
1 Capture	10	15

[a] PSF = peat swamp forest, DF = dipterocarp forest.

forest and 56% of the species netted in the dipterocarp forest (Table 3). In the Pasoh Forest Reserve, 77% of the species captured in virgin dipterocarp forest were rare (Wong 1986). In the Gunung Palung Nature Reserve, 62% of all species recorded in the peat swamp forest were insectivores; likewise, 59% of all species netted in the dipterocarp forest were insectivores. This is similar to the virgin dipterocarp forest in the Pasoh Forest Reserve, where 61% of all species netted were insectivores (Wong 1986). Of the insectivores, the preponderance of babblers (Timaliidae) is particularly striking in the Gunung Palung Nature Reserve and in the Pasoh Forest Reserve. In the peat swamp forest, 29% of the species captured were babblers, and in the dipterocarp forest 31% of the species captured were babblers. In the virgin dipterocarp forest of the Pasoh Forest Reserve, 24% of the species captured were babblers (Wong 1986). The Gunung Palung Nature Reserve and the Pasoh Forest Reserve also show similarity in the proportion of frugivores in the capture record. In both the peat swamp forest and the dipterocarp forest, 26% of the species netted were frugivores. At the Pasoh site, 19% of the species netted were frugivores (Wong 1986).

The data presented here suggest that peat swamp forests are important in the ecology of understory avian communities in Southeast Asia, even though the peat swamp forest under study produced fewer individual captures and tended towards fewer species. The peat swamp forest I sampled supported at least 34 understory bird species, including two, Gray-breasted Babbler (*Malacopteron albogulare*) (Timaliidae) and Yellow-breasted Flowerpecker (*Prionochilus maculatus*) (Dicaeidae), that strongly preferred the peat swamp forest over adjacent lowland dipterocarp forest (Table 1). There was an increase of frugivorous understory birds in the peat swamp forest in June that was correlated with an abundance of ripe fruit produced by a single tree species, *Callocarpa* sp. Without having monitored plant phenology, I cannot assume causation from this corre-

lation, but the data are suggestive. In Southeast Asian forests fruit abundance fluctuates temporally and spatially (Fogden 1972, Leighton and Leighton 1983, Wong 1986, Fleming et al. 1987), and frugivorous birds respond to these fluctuations. There is generally a positive correlation between fruit abundance and frugivorous bird abundance (Leighton and Leighton 1983, Wong 1986). The correlation between frugivorous bird abundance and fruit abundance in June in the peat swamp forest is consistent with the hypothesis that Southeast Asian peat swamp forests may act as a refuge for frugivorous animals during periods when fruit is not available in other forest habitats (Leighton and Leighton 1983). To substantiate this hypothesis, future investigators must monitor plant phenology, fruit abundance, and bird abundance simultaneously across a diversity of forest habitats.

This work is a first attempt to characterize the understory avifauna of Southeast Asian peat swamp forests, and there are limitations to the data and its analysis. First, the study is not replicated; I sampled one small stand of peat swamp forest and one small stand of lowland dipterocarp forest. Second, since I did not mark or band birds, individuals may have been captured more than once, thus violating assumptions of independence for statistical tests. Third, the reduced height of the canopy in the peat swamp forest could compress the vertical distribution of birds and result in an increase in captures of birds which dwell in the middle and upper layers of the canopy as compared to the dipterocarp forest. Finally, this study covered a brief time period and limited net hours. For example, in my study I captured 39 species during 1512 net-h over an eight-month period in the dipterocarp forest. In contrast, Wong (1986) captured 82 species of understory birds during 28,000 net-h during a 24-month period in lowland dipterocarp forest in Malaysia. To overcome such limitations in developing broad generalizations regarding the nature of peat swamp forest understory bird communities, I suggest long term studies of banded birds in the center of large tracts of peat swamp forest.

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Wilson Bull., 106(2), 1994, pp. 391–392

SHORT COMMUNICATIONS

Bird sightings from a nuclear-powered ice breaker from across the Arctic Ocean to the geographic North Pole 90°N.—Ornithologists have long speculated on which species of birds range farthest north. A prime contender has been the Ivory Gull (*Pagophila eburnea*) which seems to vanish in winter and has the ability to scavenge along leads and polynyas during that period. A recent article by J. Christopher Haney (Birding, October 1993:331–337), is the latest compiled comprehensive and useful information on that species. However, the article contains an important erroneous assumption. Haney hypothesized that Ivory Gulls range farther north than any other bird species and wander over most of the Arctic wherever pack ice is found. We challenge this assumption with the following observations.

From a starting point at Murmansk, Russia, on 15 July 1993, the Russian nuclear ice breaker *Yamal* headed northward with the objective of landing upwards of ninety tourists on the Geographic North Pole 90°N. Most at-sea sightings of birds occurred between the 70th and 80th parallels where the waters of the Barents Sea were wide open, or covered thinly with loose pack ice. Birds were conspicuous in the vicinity of the Franz Josef Archipelago (80° to 82°N) where large numbers of several species of seabirds colonize. Nevertheless, numbers of species and individuals dropped dramatically when *Yamal* entered dense pack ice, punctuated only with narrow cracks or leads, with few open areas or polynyas. These conditions occurred from about 80°52′N, 40°41′E all the way to the North Pole, attained on 21 July. The return trip was much the same. Three days were consumed each way while the ship broke ice almost constantly between the 80th and 90th parallels. The cruise terminated at Murmansk on 29 July.

Various activities aboard ship precluded regular bird observations, including traditional 10-min checks each h. Fairly regular watches were conducted during 06:00–07:00 h, 13:00–14:00, 18:00–19:00, and at odd times in between. Passengers reported their sightings. Several far northern observations were noteworthy.

*Black-legged Kittiwake (*Rissa tridactyla*).*—Most northern and abundant species encountered. Immense numbers were noted near Franz Josef islands. The species has the propensity to follow and feed in the wake of moving ships, even in dense pack ice. Flocks of kittiwakes followed the *Yamal* between the 80th and 82nd parallel. The last flock, numbering 15 individuals, was noted at 82°41′N, 39°01′E. Thereafter only single individuals were recorded, all briefly: one adult at 83°05′N, 38°21′E on 18 July, and one adult at 84°44′N, 33°59′E on 19 July. None on 20 July. On 21 July: one adult at 89°54′N, 77°50′E; one individual at 89°58′N (D. Zeilinger, P. Frautchi); and one immature at 89°58′N, 18°41′E where *Yamal* was moored in ice adjacent to the Pole. The immature, observed by many cruise participants, circled the ship several times before disappearing. These far northern sightings were not the first. Norman Laska (pers. comm.) noted a kittiwake close to the North Pole during a similar cruise in 1992.

Kittiwakes were also recorded on our return trip. On 22 July, we saw one adult at 89°09′N, 51°52′E, and one individual at 88°30′N (K. Ivinicki); on 23 July, one individual at 83°51′N (J. Sharpe); on 24 July individuals were seen frequently south of 82°00′N, 39°47′E, and the first flocks at 80°57′N, 45°09′E. Large numbers were encountered at the Franz Josef islands during 25–27 July.

Whether kittiwakes follow ships from southern latitudes all the way to the Pole is a moot question. Our limited observations indicate otherwise. Too much time elapsed between sightings of single birds, which seemingly did not follow the ship. All appeared briefly and

quickly disappeared. On several occasions they were seen catching small minnows (sp. ?), gleened from cracks in the ice, or from the ship's upwellings.

Thick-billed Murre (Uria lomvia).—Second most northern and abundant species noted. On 17 July, flocks (5–20 birds) circled the ship, but did not follow its wake. Although the flocks disappeared over thick pack ice, a few solitary individuals were noted en route to the Pole: on 19 July, one at 84°44′N, 33°59′E (P. Conway), and one at 85°30′N, 32°46′E. South from the Pole, one was noted at 87°22′N, 43°07′E on 22 July; one at 84°44′N, 33°59′E (P. Conway), and one at 85°30′N, 32°46′E on 23 July, two at 81°56′N, 32°46′E on 24 July. Small flocks were seen thereafter, notably near the Franz Josef islands. Thousands occupied precipitous cliffs at Calm Bay in the southwestern part of the Archipelago.

Black Guillemot (Cepphus grylle).—Uncommon, but the third most northern species recorded: on 24 July, over thick pack ice, one at 82°00′N, 38°47′E, one at 81°56′N, 39°49′E, one at 81°52′N, 40°01′E, and one at 80°55′N, 45°27′E. Numbers increased within Franz Josef Archipelago, especially near Cape Norway, Jackson Island.

Ivory Gull (Pagophila eburnea).—Observed only on two occasions over dense pack ice outside of the Franz Josef Archipelago where small numbers were noted. One was in the presence of a polar bear (*Thalarctos maritimus*) at 80°51′N, 40°40′E on 17 July. Most northern sighting (three birds) was at 80°55′N, 45°27′E on 24 July.

Three species of jaegers (*Stercorarius*) appeared to be fairly common over open waters of the Barents Sea (especially on 16 July at 72°54′N, 34°00′E, and on 28 July at 74°32′N, 37°24′E), but not over dense pack ice except within the Franz Josef Archipelago. Glaucous Gulls (*Larus hyperboreus*) were noted only within the Franz Joseph Archipelago, and Arctic Terns (*Sterna paradisaea*) only along the north coast of Norway.

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Hatchability of American Pipit eggs in the Beartooth Mountains, Wyoming.—Hatchability often is reported as the proportion of eggs laid that hatch. While this may be the demographic value of ultimate interest as an index of recruitment, such broad usage makes it difficult or impossible to identify more specific proximate factors affecting hatching and the extent that these may vary. Some studies note the paucity of data for comprehensive analyses of ecological and social factors influencing hatchability in wild birds (Rothstein 1973, Koenig 1982). Predation and abandonment frequently are major causes of egg loss prior to hatching, but egg infertility and embryo death may also contribute to hatching failure. These latter two conditions are of special interest because they (1) reduce potential individual reproductive success, (2) represent a substantial loss in reproductive investment by the female, and (3) can be expected to respond to selection. In theory, compensatory egg-laying could evolve in species with a high incidence of infertile eggs (Lundberg 1985), but this remains unsubstantiated and little explored. Because hatchability could be important

in the evolution of reproductive traits, the topic deserves further study, especially for a wide variety of taxa and breeding environments.

Here, we examine hatchability of American Pipit (*Anthus rubescens*) eggs at high elevations. We define hatchability as the percentage of eggs present at hatching time that produce nestlings (see Koenig 1982). In particular, we describe annual and geographic variation in hatchability for a single population breeding over a 300 m elevation gradient. We also document the relation of hatchability to (1) median date of clutch initiation, (2) nest type, (3) egg size, and (4) clutch size. Finally, we compare our results with other species nesting in tundra environments and discuss common patterns.

Study sites and methods.—Data were collected during June–August of 1987–1989 at two sites in the Beartooth Mountains, Park County, Wyoming. One site was in alpine habitat with extensive tundra lying between the two summits of Beartooth Pass (Lat. 45°0′N, Long. 109°30′W, 3200 m elev). The second site was in subalpine meadows centered around Chain Lakes (2900 m elev), about 6.4 km SW of Beartooth Pass. Verbeek (1970) and Hendricks and Norment (1992) provide additional details of the respective sites.

Eggs broken during handling or found cracked (N = 6) are excluded from our samples. Analyses of clutch trends do not include clutches where one or more eggs disappeared prior to the date of hatching, nor are numbers of predated eggs included in egg samples and analyses, except for eggs known to have failed for other reasons prior to predation (e.g., nests found with older chicks and unhatched eggs, but predated before eggs were examined for infertility or embryo death). Hatching failure of examined eggs was attributed to infertility if there was no visible development of the blastodisc, or embryo death if a visible embryo was present. Our use of the term "addled" refers to both causes of hatching failure, and hatching failure as used in this paper refers to addled eggs only. We may have overestimated the proportion of addled eggs attributable to infertility by including eggs where decomposition of the yolk had begun, but eggs with decomposing yolks occurred in less than 5% of the total sample. If we found a nest containing chicks and no eggs, we assumed all eggs hatched, as pipits do not remove unhatched eggs from nests (pers. obs.), and loss of single eggs from nests was infrequent (Hendricks, unpub. data). A total of 692 American Pipit eggs from 135 clutches was used in our analysis.

Egg volumes (V) were calculated using Hoyt's (1979) equation: $V = 0.507LB^2$, where length (L) and breadth (B) were measured with a dial caliper to the nearest 0.1 mm. To maintain sample independence, all volumes in this paper are mean values for clutches, unless specified otherwise. In some cases volumes are based on a single egg per clutch. Preston (1968) showed that size measurements from a single egg per clutch tended to be representative of the entire set.

American Pipit nests were categorized as (1) rock nests: on the ground under overhanging rocks, or (2) sod nests: on the ground under overhanging vegetation or in erosion banks, hummocks, or pocket gopher burrows (see Verbeek 1970, 1981).

Statistical procedures throughout follow Sokal and Rohlf (1981), with variation given as the mean ± one standard deviation.

Results.—Forty-eight (35.6%) of 135 American Pipit clutches contained addled eggs. In the total sample of eggs (Table 1), 67 (9.7%) of 692 failed to hatch. Thus, hatchability for the Beartooth Mountains population was 90.3% during 1987–1989. Hatchability at Beartooth Pass during that period was 90.9% (380 of 418 eggs), which was greater than that for 1963–1964 (85.9%: 286 of 333 eggs; Verbeek 1970). Of the 67 addled eggs in 1987–1989, 40 (59.7%) were infertile, 18 (26.9%) contained dead embryos, and nine (13.4%) were of undetermined contents (Table 1). Twenty-eight (34.1%) of 82 pipit clutches at Beartooth Pass, and 20 (37.7%) of 53 at Chain Lakes, contained addled eggs ($G = 0.180$, df = 1, $P > 0.5$); Verbeek's (1970) data could not be used in this analysis. Proportions varied between

TABLE 1
CAUSES OF HATCHING FAILURE AND HATCHABILITY IN AMERICAN PIPIT EGGS

	Total eggs[a]	Infertile	Embryo death	Unknown	Hatchability (%)
Beartooth Pass (3200 m)					
1987	127	7	4	0	91.3
1988	145	7	0	6	91.0
1989	146	10	4	0	90.4
Chain Lakes (2900 m)					
1987	108	7	3	0	90.7
1988	85	7	3	3	84.7
1989	81	2	4	0	92.6
Sites combined					
1987–1989	692	40	18	9	90.3

[a] Not including six eggs cracked during handling, by adults, or nests predated during incubation.

years by as much as 14.1% at Beartooth Pass ($G = 1.162$, df = 2, $P > 0.5$) and 27.9% at Chain Lakes ($G = 2.850$, df = 2, $P > 0.1$). Although these results do not show statistically significant variation, small sample size may have led to the inflated P value for Chain Lakes. The difference between sites was greatest in 1988 ($G = 2.934$, df = 1, $P < 0.1$), when 27.6% of Pass clutches and 52.9% of Chain Lakes clutches contained addled eggs. Hatchability of pipit eggs (Table 1) was virtually the same (90.2–92.6%) in all three years at both sites, except at Chain Lakes during the hot and dry summer of 1988, when hatchability was 7.2% less than the 1989 maximum.

Hatchability at Beartooth Pass was negatively correlated with the median date of egg-laying for the population (Fig. 1). In 1963 and 1964, when egg-laying was 10–18 d later (medians = 28–29 June) than 1987–1989 (medians = 10–18 June), hatchability (data extracted from Fig. 2 and Table 7 in Verbeek 1970) was 3.9–4.9% less than the minimum during 1987–1989. Comparable data were not available for Chain Lakes.

Twelve (34.3%) of 35 rock nests and 30 (37.5%) of 80 sod nests contained addled eggs ($G = 0.108$, df = 1, $P > 0.5$). For a smaller sample of nests with addled eggs of identified contents, ten rock nests (76.9%) contained infertile eggs, and three (23.1%) contained dead embryos, whereas 14 sod nests (58.3%) contained infertile eggs and ten (41.7%) had dead embryos ($G = 1.326$, df = 1, $P > 0.1$). Nest type did not influence hatchability, but dead embryos appeared in rock nests less frequently when addled eggs were present. Again, small sample size probably inflated the P value.

The difference between mean volumes of clutches with some (2177 ± 185 mm^3, N = 40) and no hatching failure (2195 ± 153 mm^3, N = 38) was slight ($t = 0.469$, df = 76, $P > 0.5$). The smallest egg was addled in ten (41.7%), and the largest egg in eight (33.3%), of 24 clutches where hatching failure occurred and all egg volumes were known. If hatching failure was a random occurrence within a clutch, then the expected number of smallest or largest eggs to fail (E_s) would be the product of the average probability of the smallest (largest) egg failing (P_s) and the total number of clutches in the sample (N), or $E_s = (P_s)(N)$. In this case, mean clutch size was 5.1 for the sample, so $P_s = 1/5.1 = 0.196$, and $E_s = 0.196 \times 24 = 4.7$. This value assumes only one egg failing per clutch. However, 1.6 eggs failed per clutch in the above sample, so the value calculated should be multiplied by 1.6,

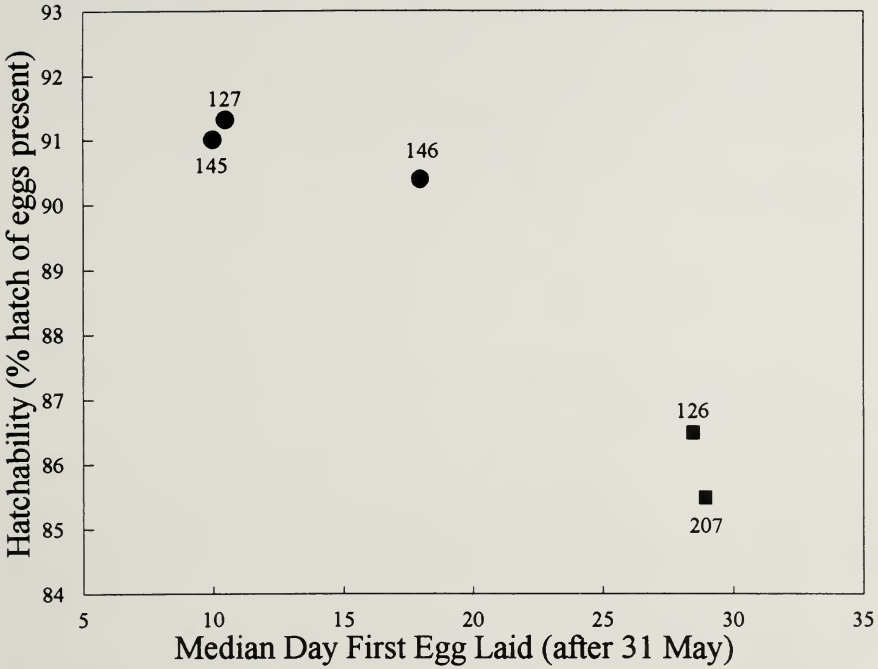

FIG. 1. Median day of clutch initiation (after 31 May) and hatchability for American Pipits nesting at Beartooth Pass (3200 m), Park County, Wyoming. Points represent single breeding seasons (squares for 1963–1964, circles for 1987–1989), and corresponding numbers are total eggs in each sample; data for 1963–1964 are extracted from Verbeek (1970).

and E_s becomes 7.5. This is only slightly different than the number of smallest ($G = 1.154$, df = 1, $P > 0.2$) or largest ($G = 0.053$, df = 1, $P > 0.5$) addled eggs. The proportion of smallest and largest addled eggs in this sample was similar ($G = 0.360$, df = 1, $P > 0.5$), further indicating that hatchability was independent of egg size.

However, egg volume was important in determining the type of hatching failure. Mean volume of infertile eggs (2128 ± 203 mm^3, N = 24 clutches) was 6.3% less than eggs with dead embryos (2270 ± 167 mm^3, N = 12 clutches; $t = 2.091$, df = 34, $P < 0.05$). Infertile eggs ranged from 1809–2488 mm^3 (N = 14) at Chain Lakes and 1635–2636 mm^3 (N = 24) at Beartooth Pass. Respective ranges for eggs with dead embryos were 1822–2601 mm^3 (N = 10) and 2136–2555 mm^3 (N = 8).

Clutches containing addled eggs were not appreciably larger (5.2 ± 0.7, N = 47) than those with none (5.0 ± 0.9, N = 87; $t = 1.042$, df = 133, $P > 0.2$). In nests with addled eggs, clutch size did not differ between those containing infertile eggs (5.3 ± 0.6, N = 24) and dead embryos (5.3 ± 0.5, N = 13; $t = 0.101$, df = 35, $P > 0.9$). The proportion of clutches experiencing some hatching failure increased slightly with clutch size (by 9.5%) for four- to six-egg clutches (Table 2), but the differences were not significant ($G = 0.528$, df = 2, $P > 0.5$). Hatchability remained constant over that same range of clutch sizes.

Of 48 clutches with some hatching failure, 14 (29.2%) involved more than one egg, but the occurrence of multiple addled eggs varied little from four-egg (33.3%) to six-egg

TABLE 2

CLUTCH SIZE OF AMERICAN PIPITS AND THE NUMBER OF CLUTCHES WITH UNHATCHED EGGS

	Number of unhatched eggs/clutch[a]					Proportion hatch failure	
	0	1	2	3	4	Clutches[b]	Eggs
Clutch size							
3	5[c]	1	—	—	—	0.167	0.056
4	14	4	2	—	—	0.300	0.100
5	44	18	7	1	—	0.371	0.100
6	23	11	1	2	1	0.395	0.101
7	1	—	—	—	—	0.000	0.000

[a] Not including nests with cracked eggs.
[b] With one or more unhatched eggs.
[c] Number of clutches.

(26.7%) clutches ($G = 0.120$, df = 2, $P > 0.5$). Also, the observed distributions of addled eggs within four- to six-egg clutches differed little from expected (binomial tests; $P > 0.2$). In only one of nine clutches containing multiple addled eggs of known contents was hatching failure due to both infertility and embryo death ($G_{adj.} = 5.869$, df = 1, $P < 0.05$). There were no known cases where entire unabandoned clutches failed as a result of infertility or embryo death or both (Table 2).

Discussion.—Several ecological and social patterns in hatchability have been identified for natural populations. Koenig (1982) found hatchability to be a function of nest type (open or cavity), diet, latitude, and the degree of sociality in an analysis of 155 studies representing 113 species.

Overall hatchability (Table 1; 90.3%) of American Pipit eggs at our two sites fell within the range of 80.4–94.0% for other passerines (Ricklefs 1969, Dixon 1978, Morin 1992), and was almost Koenig's (1982) predicted percentage for the latitude of our study sites. Hatchability was much lower (84.7%) below treeline at Chain Lakes in 1988 than for other years at either site during our three-year study, and was the only sample for which hatchability was <90.0%. Increased incidence of addled eggs at Chain Lakes in 1988, the summer of extensive wildfires in Yellowstone National Park about 35 km away, may have been the result of hot and exceptionally dry conditions for the region (Singer et al. 1989). Chain Lakes, 300 m lower than Beartooth Pass, normally experiences daily maximum temperatures 2–4°C higher (Hendricks and Norment 1992). High temperatures are injurious to developing embryos, and exposure of eggs to direct sunlight (when females are off of the nest) can kill embryos even though air temperatures may be relatively cool (Zerba and Morton 1983, Morton and Pereyra 1985, Webb 1987); ground-level temperatures at high elevations can exceed air temperatures by >20°C (Swan 1952, Hadley 1969) and may add thermal stress to incubating females of ground-nesting species, such as the American Pipit. It is possible that several eggs considered infertile in 1988 actually contained embryos that died in the first day or two of development and were misclassified. Regardless of this possibility, there was an association between a greater incidence of addled eggs and unusually warm weather at the subalpine site.

In contrast with Rothstein (1973), at Beartooth Pass we found a higher incidence of addled eggs produced by American Pipits during years with delayed egg-laying and lingering snowpack (Fig. 1). This pattern might be related to differences in food availability or quality, or

the maintenance energy and protein demands on females during and after egg-laying (see Martin 1987). Unfortunately, direct measures of food abundance at Beartooth Pass during the breeding season are not available for 1963–1964; maximum arthropod abundances did not differ greatly during 1987–1989 (Hendricks, unpub. data). During the initial week of laying in 1987–1989, mean clutch size was identical (5.5; Hendricks, unpub. data) and hatchability ranged from 90.4–91.3%. In 1963–1964, when hatchability was <87%, clutch size during the first nine-day laying period was 4.7 (Verbeek 1970). Females waiting to lay for extended periods (as in 1963–1964) may lose important energy and protein reserves, resulting in the production of a greater proportion of lower quality or infertile eggs (see Blem 1990). Also, females may have to spend more time foraging away from nests to satisfy maintenance energy demands because of cooler initial and average conditions during late years. This could result in eggs cooling to lethal temperatures from inefficient incubation (Pinowski 1968). Hatchability of Harris' Sparrow (*Zonotrichia querula*) eggs in the Northwest Territories of Canada was lowest (78.9%) during a year when conditions during laying were cooler and wetter than in other years (Norment 1992).

Similar to other studies (Koenig 1982, Bancroft 1984, Briskie and Sealy 1990), we found that hatchability and size of American Pippit eggs were not correlated. Volume varied significantly between sites in 1989 (Hendricks 1991) but did not correspond to a large difference (2.2%) in the occurrence of addled eggs. Conversely, the difference in hatchability between sites increased to 6.3% in 1988, but the difference in mean egg volume was not significant ($t = 0.040$, df = 45, $P > 0.9$; Hendricks, unpub. data). This is consistent with the hypothesis that temperature, rather than egg size, had a deleterious effect on hatchability of pipit eggs at Chain Lakes in 1988.

Unlike hatchability, the contents of addled eggs were related to egg size; infertile eggs were smaller than eggs containing dead embryos. Perhaps smaller eggs were more likely to lack membranes or the proper ratio of albumen to yolk needed for fertilization and development, as is the case with runt eggs (e.g., Koenig 1980a, b), but infertility was probably a function of several factors. Absolute size (volume) was not the sole determinant of infertility, as the size range of infertile pipit eggs (1635–2636 mm^3) was large and overlapped the range of fertile eggs (see Hendricks 1991). Our results were unaffected by runt eggs; volume of the smallest egg in our sample (1635 mm^3; infertile with a yolk) was 85.9% of the clutch mean for the other five eggs, all of which hatched. No egg fell under Koenig's (1980a) 75% relative size criterion for runts.

Infertile eggs comprised a greater proportion (5.8%) of our three-year American Pipit sample from high-elevation tundra than the 1.2–2.6% for several passerine species nesting in high-latitude tundra at Churchill, Manitoba during a four-year study (Jehl 1971). Hatchability for Lapland Longspurs (*Calcarius lapponicus*) at Barrow, Alaska, also a high-latitude tundra site, was 93.0% (88.8–98.5%) during a seven-year study (Custer and Pitelka 1977), a slightly better performance than for Beartooth pipits (90.3%) and greater than the range of values at Beartooth Pass (Fig. 1). However, longspur hatchability during two years of very different weather in West Greenland was 85.4–86.6% (Fox et al. 1987). Hatchability of Harris' Sparrows in the Northwest Territories of Canada averaged 87.6% (78.9–93.4%) during three years (Norment 1992). These data show that hatchability can be heterogeneous among years at one locality, and that conclusions on species-specific hatchability based on small samples of eggs or breeding seasons could be misleading. Nevertheless, overall hatchability appears to be similar for passerines breeding in mid-latitude and high-latitude alpine and Arctic tundra.

Hatchability tends not to be a function of elevation (Carey et al. 1982, Koenig 1982), although the number of studies on single species is small. Our data for American Pipits over a 300 m elevation gradient showed that hatchability was relatively uniform during

breeding seasons of cool weather. However, hatchability below treeline during hot years may be lower than in the alpine, as was the case in the Beartooth Mountains in 1988, because temperature maxima are more extreme in high-elevation subalpine meadows. It would be interesting to see if hatchability is increased for American Pipits nesting at low-elevation high-latitude sites.

Orientation of Beartooth pipit nests protects eggs from exposure to direct sunlight and its detrimental effects on embryo development (Verbeek 1981, Zerba and Morton 1983, Morton and Pereyra 1985), and hatchability was unrelated to nest type. However, in spite of small samples, eggs in sod nests appeared more susceptible to embryo death. If this is really the case, overcooling during periods of foul weather could contribute to this pattern (see Hendricks and Norment 1992); lowest hatchability (78.9%) of Harris' Sparrows, which build cup nests on the ground under overhanging vegetation, occurred when weather during laying was cooler and wetter than in other years (Norment 1992). Overhanging grasses and turf provide less overhead protection from precipitation to nests than does rock, even though grass is a better insulator (Collias and Collias 1984).

Koenig's (1982) broad analysis showed that species building ground and open-cupped nests had greater hatchabilities than shrub, tree, and closed (cavity) nesters. Koenig (1982) suggested that a greater proportion of inexperienced females, with reduced hatchabilities during first breeding attempts, might be included in samples for species relatively protected from predators, such as cavity-nesting woodpeckers; experienced, older females are less likely to be predated in species normally experiencing high rates of predation, such as ground nesters. This tells us little about single species, however, and emphasizes the need for further studies on the influence of nest placement on intraspecific geographic patterns of hatchability.

Hatchability was unrelated to clutch size in our study of American Pipits (Table 2), a result also observed for other species (Rothstein 1973, Koenig 1982, Lundberg 1985, but see Briskie and Sealy 1990). Also, the proportion of clutches containing addled eggs increased only slightly with clutch size, and multiple addled eggs appeared in nearly equal frequencies among four- to six-egg clutches. If clutch size has any influence on hatching success of pipit eggs, the effect is apparently minor.

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Phthiraptera infestation of five shorebird species.—Chewing lice (Insecta: Phthiraptera) are a potentially important influence on the ecology and behavior of birds. Lice reduce host survival by increasing energetic costs (Booth et al. 1993) and by transmitting endoparasites and pathogens (Clayton 1990). Lice also influence reproductive success of birds by rendering individuals less attractive as mates (Clayton 1990) and by reducing fecundity (DeVaney 1976). Despite their importance, knowledge of variation in louse infestation is generally lacking. In fact, few studies have produced systematic surveys of lice across closely related bird taxa (but see Clayton et al. 1992). Accordingly, we sampled chewing lice from five shorebird species (Black Turnstone [*Arenaria melanocephala*], Western Sandpiper [*Calidris mauri*], Least Sandpiper [*C. minutilla*], Dunlin [*C. alpina*], and Long-billed Dowitcher [*Limnodromus scolopaceus*]) to assess interspecific and intraspecific variation in ectoparasite infestation.

Study area and methods.—We mist-netted shorebirds from 12 Sept.–24 Oct. 1992 within the Mad River estuary, about 8 km northwest of Arcata, California (40°56′N, 124°07′W). For a description of the study site see Colwell and Landrum (1993). To standardize our sampling of lice, one of us (JEH) conducted constant effort (5 min) searches of an area of the head (including the forehead, crown, and hindhead) bounded by imaginary lines running through anterior and posterior corners of the eyes (crown count; equivalent to the crown region of Eveleigh and Threlfall 1976). Using forceps, we removed lice and preserved them in 70% ethyl alcohol.

The use of area and time-constrained searches to produce indices of ectoparasite occurrence provides a feasible alternative to more intense or complicated methods (Marshall 1981). We used this type of sampling because it reduced handling time and did not require use of insecticides or necessitate that hosts be killed. We sampled the head region because it was readily accessible for sampling. In addition, a reduced ability of birds to preen the crown may result in a relatively higher density of lice (Stock and Hunt 1989), which would result in a larger proportion of the total parasite load being sampled than would be at another location on the host. However, this method may result in biased data (species lists and abundance for hosts) for chewing lice for several reasons. Louse species tend to concentrate on different body regions of the host (Marshall 1981). Consequently, some louse species may be overlooked, and the total number of lice on a bird may not be correlated with abundance in the head region (Eveleigh and Threlfall 1976, Choe and Kim 1988). In addition, on 10 of the birds we examined, we observed lice but failed to collect any during the 5-min sampling period. This suggests that our method may not be useful for sampling some of the more mobile species or age classes of lice. We also observed lice on other body parts or on our hands during processing of two of nine birds with crown counts of 0. Thus, a crown count of 0 does not necessarily indicate a complete absence of lice, only that the number of lice on that host was relatively low. Taken together, these observations suggest that our estimates of prevalence and abundance are conservative, and our results should be interpreted cautiously and with reference to the head region only. Despite these limitations, our standardized methodology produced data useful for direct comparisons between shorebirds.

For each shorebird species, we estimated louse prevalence as the percent of birds infested with at least one louse (Clayton et al. 1992); we indexed relative abundance as the average (± SE) number of lice per individual (head). We examined interspecific differences in abundance using a Kruskal-Wallis test (Zar 1974). To evaluate the null hypothesis of random distribution of lice among individuals of a given species (*Calidris* species only), we compared observed patterns against a Poisson distribution using Chi-square goodness-of-fit tests (Ludwig and Reynolds 1988). Finally, we compared louse community composition between

bird species using Renkonen's percent similarity index, a measure less sensitive to sample size variation and low species diversity than other similarity indices (Wolda 1981).

Results and discussion.—Eighty-six percent of the 65 shorebirds we examined had lice. Calidridine sandpipers exhibited the highest parasite prevalence (85–92% of individuals infested), and Long-billed Dowitcher and Black Turnstone had lower values (75 and 66%, respectively; Table 1). The relatively high prevalence values we observed for scolopacids, compared with some other bird species (e.g., Clayton et al. 1992), was not surprising because shorebirds are highly social and lice are transmitted between hosts via direct body contact (Marshall 1981).

Louse abundance (Table 1) did not differ significantly among shorebird species (Kruskal-Wallis test: $H = 4.6$, df = 5, $P = 0.33$). Although louse abundance may be influenced by molting (Marshall 1981), we observed no interspecific difference in louse numbers despite marked interspecific variation in molt patterns between shorebird species.

Composition of louse communities differed between shorebird species (Table 1). Of seven louse species collected, four occurred exclusively on one shorebird species. All louse species collected had previously been recorded from these birds (R. Price, pers. comm.). Congeneric shorebirds shared more louse species (50%, 24%, and 0% similarities between *Calidris* species) compared with shorebirds from different genera (no shared taxa). These data corroborate Fahrenholz's rule, which states that classification of permanent parasites (those completing their entire life cycle on a host) corresponds to the taxonomic relationships of hosts (Marshall 1981). In other words, as host organisms and their parasites coevolve, parasite communities track the cladogenic development of host groups. Relationships between host and parasite phylogenies are well documented, especially in the highly host-specific chewing lice and their bird hosts (Rothschild and Clay 1957, Marshall 1981). Clay (1962) noted that species within the subfamilies (Vanellinae and Charadriinae) of Charadriidae exhibited greater similarities in chewing lice (*Actornithophilus*) compared with species from different subfamilies. Interspecific (host) differences in louse communities have been studied in other charadriiforms as well. Choe and Kim (1987) found that louse communities of congeneric seabirds (Black-legged Kittiwake [*Rissa tridactyla*] and Red-legged Kittiwake [*R. brevirostris*]; Common Murre [*Uria aalge*] and Thick-billed Murre [*U. lomvia*]) were quite similar, whereas host species from different genera shared no chewing lice species.

Lice were nonrandomly distributed (clumped) among Least Sandpipers ($\chi^2 = 20.2$, df = 9, $P < 0.05$) and Western Sandpipers ($\chi^2 = 16.7$, df = 5, $P < 0.05$), but not Dunlins ($\chi^2 = 1.1$, df = 2, $P > 0.05$). With the exception of studies describing louse infestation of eggs (e.g., Rankin 1982), it appears that no report of systematic measurement of shorebird (Charadrii) chewing lice has been published; most available information is anecdotal. For example, Marshall (1981) reported that 3427 lice were removed from eight Eurasian Oystercatchers (*Haematopus ostralegus*), and Meinertzhagen and Clay (1948) found 3–11 lice on each of seven primaries of a Eurasian Curlew (*Numenius arquata*). Taylor (1981) suggested that the adventitious molt he observed in a Red Knot (*Calidris canutus*) was the result of feather damage caused by lice. Rothschild and Clay (1957) reported that Eurasian Curlews typically have 50–200 lice, although a few had none, and one individual had 1803. Host health and preening ability (Rothschild and Clay 1957, Clayton 1990), along with the same factors which affect louse prevalence and abundance, may also be important in determining individual parasite loads.

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TABLE 1

LICE INFESTATION OF FIVE SHOREBIRD SPECIES

Louse taxon	Black Turnstone (N = 3)	Western Sandpiper (N = 20)	Least Sandpiper (N = 25)	Dunlin (N = 13)	Long-billed Dowitcher (N = 4)
Family Philopteridae					
Quadraceps strepsilaris (Denny)	10[a]	0	0	0	0
Saemundssonia tringae (O. Fabricius)	0	34	0	7	0
Carduiceps zonarius (Nitzsch)	0	37	96	0	0
Carduiceps meinertzhageni Timmermann	0	0	0	21	0
Carduiceps cingulatus (Denny)	0	0	0	0	5
Family Menoponidae					
Actornithophilus umbrinus (Burmeister)	0	4	1	0	0
Austromenopon alpinum Timmermann	0	0	0	1	0
Prevalence	66%	85%	92%	85%	75%
Louse abundance (±SE)	3.3 ± 2.0	3.8 ± 0.7	3.9 ± 0.6	2.2 ± 0.4	1.3 ± 0.6

[a] Numbers indicate total number of lice collected from each shorebird species.

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Double brooding in Red-cockaded Woodpeckers.—In 1991, seven groups of the cooperatively breeding Red-cockaded Woodpecker (*Picoides borealis*) produced second broods after successfully fledging young from first broods. These seven groups were in three different populations, five in the sandhills of North Carolina, one in the sandhills of South Carolina, and one in coastal North Carolina. No previous observation of double brooding

has been reported in this endangered species, despite intensive observations over the past 20 years over most of the range. In this note, we provide details of this unusual phenomenon.

Double brooding is common among bird species in the southeastern United States, including woodpeckers. Among other species in the same genus, the Downy Woodpecker (*P. pubescens*) may produce a second brood in this region, but the Hairy Woodpecker (*P. villosus*) is not known to be double brooded (Bent 1939). In other woodpecker genera, such as *Melanerpes* and *Sphyrapicus,* double brooding may be common (Bent 1939, Short 1982, Ingold 1987), but it occurs in only 4.9% of groups of the cooperatively-breeding Acorn Woodpecker (*M. formicivorous,* Koenig and Mumme 1987). Thus the occurrence of double brooding in Red-cockaded Woodpeckers is expected on taxonomic or geographic grounds. It is, however, somewhat unexpected on behavioral grounds, as temperate zone cooperative breeders generally are not double brooded. Indeed the species' nesting habits had been so thoroughly studied over such a long period without observation of double brooding that it frequently has been stated as fact that double brooding is not a part of the species' biology (e.g., USFWS 1985, Walters 1990).

Even in 1991, double brooding in Red-cockaded Woodpeckers was a rare phenomenon. Among 193 nesting groups monitored in the North Carolina sandhills, only five second broods were recorded (Fig. 1). In the South Carolina sandhills population, only one of six groups attempted a second brood, and in the North Carolina coastal population, only one of 42. Double brooding was discovered independently within the three populations, but was not observed in a second, nearby coastal population in North Carolina that we also monitored, nor in another South Carolina population, a Georgia population, and two Florida populations monitored by others. We think it unlikely that double brooding occurred but was overlooked in these populations in previous years, except perhaps as isolated instances. In the North Carolina Sandhills, one second brood was discovered during a normal visit to confirm group composition and another when a group was revisited because the breeding adults were observed copulating during a check for fledglings from the first nest. After these discoveries, nearly all groups that successfully fledged young by 15 June were checked for possible second broods. This indicates that if, in previous years, double brooding occurred at even the low frequency observed in 1991, normal nest monitoring procedures (described by Walters et al. 1988) and behavioral observations should have been sufficient to detect it.

The North Carolina sandhills study area (NCS) is described by Carter et al. (1983) and Walters et al. (1988), and the South Carolina sandhills population, located at the Savanna River Site (SRS) by Jackson (1984) and Gaines et al. (in press). The North Carolina coastal population is located on Croatan National Forest (CNF) and is the northernmost population of Red-cockaded Woodpeckers of even modest size.

All five second nests in NCS were successful, as was the single second nest at SRS. The sole second nest at CNF failed during the nestling stage. The number of young fledged from second nests was small (1–2) compared to the number (1–4) fledged from first nests in the same groups (Table 1). At NCS, second broods were produced by pairs that initiated their first nests relatively early in the breeding season. The five groups that produced second broods were among the first 16 to nest in the population, and four were among the first 11 to nest (Fig. 1). Birds in the northwestern quarter of the NCS study area nest slightly earlier than the other birds. Two of the groups that produced second broods were in this area, and they were among the first three groups in this area to nest. The three remaining groups that produced second broods were among the first seven outside the northwestern area to nest. Second broods were initiated 7–23 June compared to initiation dates for second attempts, by groups that failed initially, that ranged from 9 May to 19 June.

Breeding females in double-brooded groups were relatively old (4–9 yr, median 7 yr; Table 1) compared to other breeding females in the NCS population in 1991 (median age:

TABLE 1

NUMBER OF FLEDGLINGS PRODUCED IN FIRST AND SECOND BROODS OF RED-COCKADED WOODPECKERS FOR SEVEN GROUPS IN 1991

	Fledglings produced						
	First brood		Second brood		Breeder age (yrs)		Number of helpers
	Male	Female	Male	Female	Female	Male	
NCS 1	0	2	0	1	4	8	1
NCS 2	0	4	1	0	7	>7	3
NCS 3	0	3	0	1	6	7	0
NCS 4	1	2	1	0	9	5	2
NCS 5	1	1	1	1	9	5	0
CNF	1	0	failed		>3	>3	2
SRS	1	0	1	0	3	4	0

3 yr; Fig. 2). They tended to be the oldest females among those that nested early. Six of the 16 earliest nesting females were more than four years old, and four of these produced second broods. The two old females that did not produce second broods nested relatively late among these early nests and were located in the northwestern area. Four of the five females disappeared from the population and were presumed dead before the 1992 breeding season (yearly mortality for NCS females is 31.4%: Walters et al. 1988; and for females

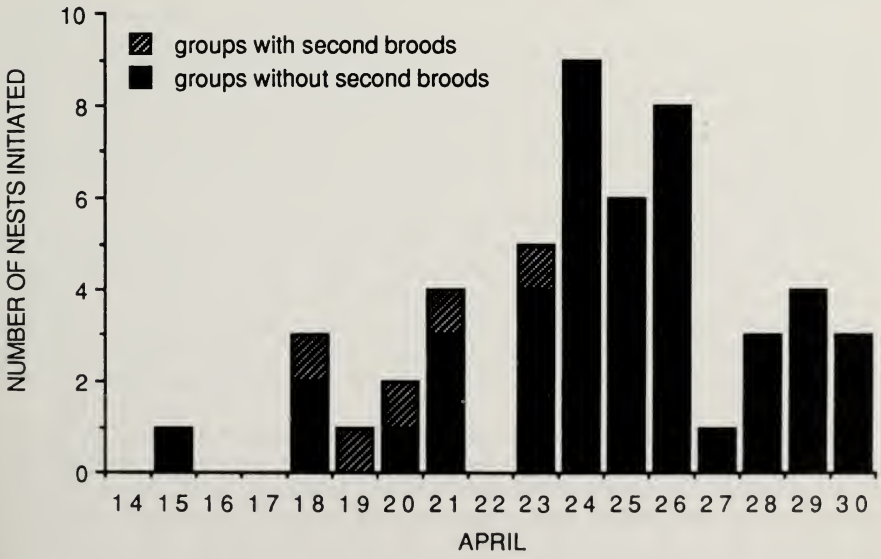

FIG. 1. Distribution of nest initiation dates for nests initiated in the North Carolina sandhills in April 1991. Initiation dates were calculated by back-dating from the date of hatching.

FIG. 2. Distribution of ages of breeding females in 1991 in the sandhills of North Carolina.

four years old and older is 35%; unpubl. data). Breeding males in these groups, on the other hand, were not older than average (4–7, Table 1; population median age 5 yr) and all were seen in the following season (yearly mortality for breeding males is 24%, Walters et al. 1988). Three of the NCS groups included helpers, whereas two did not (Table 1). First broods produced by these groups were female biased, whereas second broods had an even sex ratio (Table 1).

It is difficult to characterize groups that attempted second broods in the other two populations, since only one instance occurred in each. However, the characteristics of those groups (early first nest, older breeding female) are at least consistent with what was observed at NCS. Among the 41 other CNF groups, 10 nested as early as the group that attempted a second brood. Most of the breeding females at CNF were of unknown age. At SRS, the group that produced a second brood was the second of the six groups to initiate a first nest. The breeding female in this group was three years old, the median age for females in the population (Table 1).

In NCS, older females generally nest earlier in the season than do first year females and early nests are less likely to fail than later ones (LaBranche and Walters, unpubl. data). When early nests fail, renesting often occurs, but the last date at which renesting may be initiated varies greatly among years, occurring in early June in some years, but not until mid-July in others. The percentage of groups with failed nests that attempt renesting has varied from 7 to 48% between 1980 and 1991. At CNF this percentage has varied from 0 to 40% in the three years it has been studied (1989–1991). Another aspect of reproductive biology that varies from year to year is the percentage of groups nesting. Each year some groups do not attempt even a first nest. Usually these groups have a young breeding male

(Walters 1990). The proportion of groups that did not nest has varied from 4 to 20% in NCS, and from 5 to 12% at CNF.

The proportion of groups nesting and the likelihood of renesting are independent aspects of nesting effort. For both aspects, nesting effort was great in 1991. At NCS, both percentage of groups nesting and probability of renesting were the second highest levels observed between 1980–1991. Only one other year, 1984, was comparable, but there is no evidence (based on winter censuses and presence of unbanded helpers in 1985) to suggest that double brooding occurred. On CNF, both percentage of groups nesting and probability of renesting were by far the highest levels observed during the three years the population has been studied. Annual variation in reproductive parameters, such as these nesting effort parameters, appears to be highly correlated among populations within the Carolinas. For example, in 1991 the coastal North Carolina population at Camp LeJeune also experienced the highest proportion of groups nesting and greatest frequency of renesting observed in six years of study (96% and 40% respectively, compared to previous ranges of 81–93% and 0–33%). It appears that in this species the upper extreme of effort includes occasional double brooding, but that this level is not reached in most years. In NCS, double brooding may have occurred but been overlooked in 1984 and perhaps 1987, but otherwise during the years since 1980, nesting effort has not approached the level at which double brooding might be expected to occur. The two coastal populations had not reached these levels at all previously during the period 1986–1990. We have not noticed obvious differences in weather between years of high effort and years of low effort. The only unusual characteristic of the 1991 breeding season that we can discern is that it followed two successive mild winters.

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Direct use of wings by foraging woodpeckers.—Wing use in food-gathering activities has not been observed frequently in birds; the direct use of wings in foraging appears to be quite rare. We define direct wing use as the use of wings in behaviors directly involved in food item "capture" and retention. In contrast, indirect wing use is characterized by the use of wings in behaviors related to, but not directly involved in, food item capture. Here we describe direct use of wings by four species of woodpeckers. These observations, combined with scattered references to similar behavior in other woodpecker species (MacRoberts and MacRoberts 1976, Jackson 1983), bring the total number of woodpecker species in which direct use of wings has been observed thus far to six. We discuss these observations in the context of general patterns of wing use in avian foraging, as well as with respect to speculated evolutionary pathways to avian flight, some of which hypothesize foraging as a function of the avian "proto-wing".

We observed direct wing use in foraging by free-ranging woodpeckers during a series of experiments examining tradeoffs between foraging behavior and vigilance. Experiments were conducted by the senior author in a mature 20-ha deciduous woodlot in western Vigo County, Indiana, from January through March 1993. Woodpeckers had free access to 1-m long sassafras (*Sassafras albidum*) logs. In each log, 1-cm diameter holes were drilled at 5-cm intervals; these holes were filled with purified beef fat before each experimental session. The beef fat provided an essentially non-depleting food resource for the birds (Lima 1992). Logs were aligned 1.5 m apart and were presented in one of four possible pair-wise combinations of diameter (1.5 and 20 cm) and orientation (horizontal and vertical). Approximately 35 h of observations were videotaped from a house through a camouflaged window at a 10-m distance in March 1993. A filming session began at dawn and lasted for approximately 100 min. Behavior was recorded at the equivalent of 30 frames/sec. Woodpecker species foraging on experimental logs were Downy Woodpeckers (*Picoides pubescens*), Hairy Woodpeckers (*P. villosus*), Red-bellied Woodpeckers (*Melanerpes carolinus*), Red-headed Woodpeckers (*M. erythrocephalus*), Pileated Woodpeckers (*Dryocopus pileatus*), and Northern Flickers (*Colaptes auratus*). Other species feeding on the logs were Carolina Chickadees (*Parus carolinensis*), Tufted Titmice (*P. bicolor*), White-breasted Nuthatches (*Sitta carolinensis*), and Carolina Wrens (*Thryothorus ludovicianus*).

"Wing-catching" of food items was observed in Downy, Hairy, Red-bellied, and Pileated woodpeckers. Wing-catching refers to the extension of a wing to prevent a food item (in

this study, a fat fragment) from falling to the ground. Fig. 1 shows a Red-bellied Woodpecker in lateral view on a vertical surface, performing a typical wing-catching sequence. After a series of pecks had dislodged a fat fragment (Fig. 1A), the bird typically probed with its tongue to extract the item. If the item was dropped, or ricocheted from the force of a peck, a wing-catching attempt was made. This consisted of retraction of both metatarsi, pulling the breast into the tree-truck (Fig. 1B), forward extension of the radius-ulna to capture the food item (Fig. 1C), and retrieval of the food item with the bill (Fig. 1D). Only one wing was extended at a time, always on the side of the dropped food item; there was little or no spreading of the primaries. This basic sequence was similar when performed on a horizontal surface, but was observed only once (for the resident female Pileated Woodpecker), although birds dropped or spilled food as often as they did on a vertical surface. This behavior was most prevalent during cold days (<0°C); at low temperatures, the beef fat was brittle, and it often fragmented after the bird delivered a blow with its bill. The frequency of wing-catching behavior was thus a function of the extent to which the beef fat fragmented, but each wing-catching species performed this behavior at least once each session, and often several times per feeding bout. Wing-catching was not observed in either Red-headed Woodpeckers or Northern Flickers, despite repeated opportunities to do so.

The direct use of wings in feeding has been mentioned for Acorn Woodpeckers *M. formicivorous* (MacRoberts and MacRoberts 1976) and for captive juvenile Red-cockaded Woodpeckers *P. borealis* (Jackson 1983). In both species, the wings were extended to catch dropped food; Acorn Woodpeckers apparently use the "pocket" formed by the wing and breast against the branch surface to "capture" dislodged acorns (MacRoberts and MacRoberts 1976). Other species of woodpeckers have been observed to use their breast to manipulate food items. Although wing involvement was not mentioned, both Red-bellied and Crimson-crested (*Campephilus melanoleucos*) woodpeckers have been observed to trap dislodged and falling food items between the breast and the tree-truck (Kilham 1972, 1983). We observed the use of the breast to trap food by most woodpecker species in our study, including Red-headed Woodpeckers, which were not observed to wing-catch. Neither behavior was observed for flickers, suggesting that these types of food manipulation behaviors may be restricted to more arboreal species. For woodpeckers in general (and possibly other species of bark-foragers), it seems likely that capture and retention of food items by either the breast or the wings, or both, would be observed during natural foraging, since dropping prey items (such as wood-boring larvae) during extraction appears to be fairly common (Kilham 1972, 1983).

Indirect use of wings in foraging has been documented much more frequently than direct wing use. Such behavior has been suggested for the Northern Mockingbird (*Mimus polyglottos*) and for several species of herons (Ardeidae). Evidence suggests that wing-flashing in mockingbirds is a behavior which startles prey and thus increases prey accessibility (Hailman 1960). Herons show a much greater diversity in wing use during feeding. Like wing-flashing, "wing-flicking" by herons may serve to startle prey. Presumably, the "canopy" posture and "tenting" behaviors, exhibited by egrets and the Black Heron (*Egretta ardesiaca*) respectively, increase prey visibility in the highly reflective aquatic environment (Meyerriecks 1962, Hancock and Kushlan 1984, Welty and Baptista 1988). However, because prey items are not directly retained or manipulated by the wings in these species, these behaviors are clearly in a different category from those performed by foraging woodpeckers.

The observations reported here for woodpeckers will be useful for evaluating the role of wings in early avian species such as *Archaeopteryx*. Although purely conjectural, the so-called "insect-net" behavior of *Archaeopteryx* is probably the most famous example of direct wing involvement in foraging. Ostrom (1974) suggested that the *Archaeopteryx* "pro-

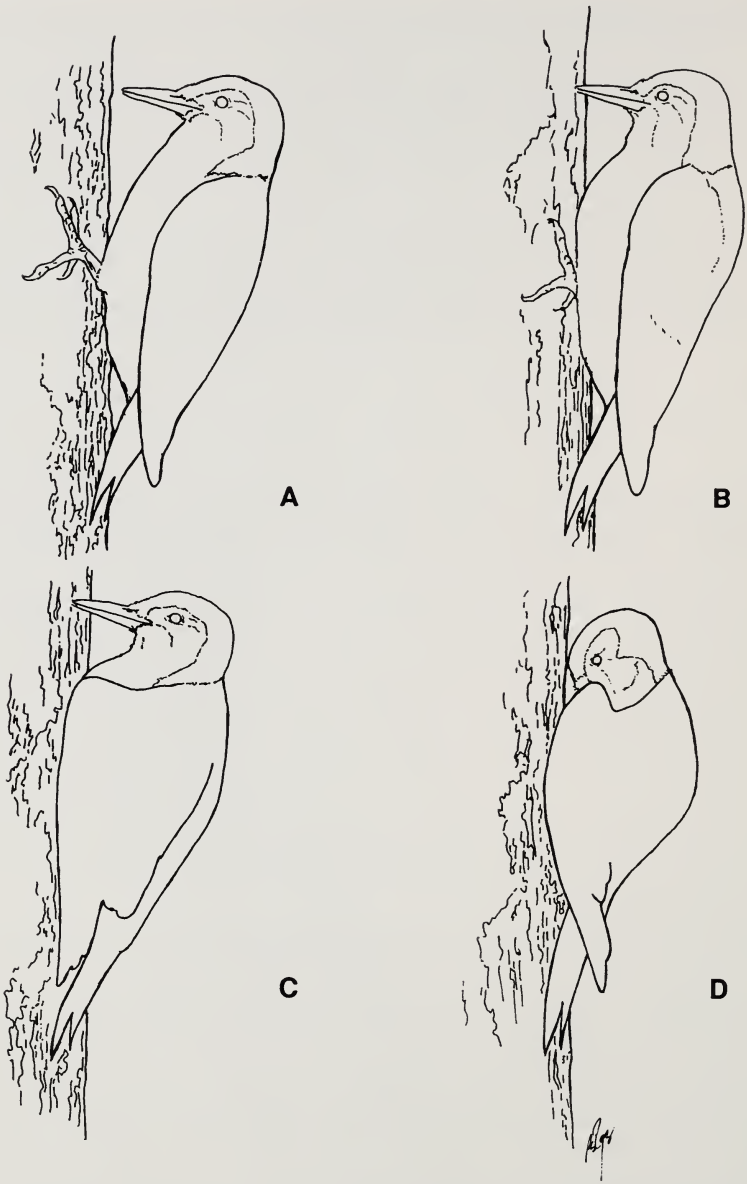

FIG. 1. Typical wing-catching sequence in a Red-bellied Woodpecker. Sequential postures at 0.2-sec intervals. See text for details.

to-wing'' was used as a snare to surround or corral small prey, such as insects and small reptiles. However there are two main objections to this theory. First, although wing use in agonistic or aggressive encounters or for balance is cited as support, there has been no direct analogue to insect-net behavior reported for living bird species. Second, the ''net'' analogy itself has been considered inadequate; presumably feather structure, while adequate for retaining prey items, would not allow sufficient air passage as would be observed in an actual net (Bock 1986). However, woodpecker behavioral analogues suggest that the feathered wings of *Archaeopteryx* would be appropriate for a less-active ''cupping'' behavior or a pounce onto active small prey, especially if the concept of *Archaeopteryx* as an arboreal climber and percher is correct (Feduccia 1993).

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Does use of doubly labeled water in metabolic studies alter activity levels of Common Poorwills?—The doubly labeled water (DLW) technique is the major method currently used to estimate field metabolic rates (FMR) in free-ranging animals (Lifson and McClintock 1966, Speakman and Racey 1988a, Nagy 1980). The procedure involves injecting small amounts of radioactive or stable isotopes (^{3}H or ^{2}H and ^{18}O). After the isotopes have equilibrated with body water, a blood sample is taken. The animal is then released, and a second blood sample is taken one to several days later. Measurements of isotopic loss then provide a means of estimating CO_2 production, from which FMR can be calculated. Validation studies suggest that DLW provides an estimate of FMR accurate to 5–10% in vertebrates (Nagy 1980, 1989; Nagy and Costa 1980; Williams and Nagy 1984a, b; Goldstein and Nagy 1985; Speakman and Racey 1988b; Nagy et al. 1990; Gabrielsen et al. 1991). To our knowledge, the only rigorous assessment of the effect of the DLW protocol (e.g., injection, holding in captivity during equilibration, and blood sampling) on behavior, and hence energy expenditure, has been done under laboratory conditions (Speakman et al. 1991). These authors call for an assessment of the protocol on free-ranging animals.

We made an independent set of measurements to determine if the injection, equilibration period, and blood sampling associated with the DLW technique alters foraging activity of free-ranging Common Poorwills (*Phalaenoptilus nuttallii*). We used telemetry and chose to measure feeding activity as an indicator of altered behavior, since this is probably the most energetically costly behavior undertaken by these birds and because it is easily assessed using telemetry. Poorwills are nocturnal insectivorous birds which have the ability of enter torpor (Brigham 1992), making them interesting subjects for energetic studies. However, since entry into torpor would confound estimates of activity, we collected data only for incubating and brooding birds who do not usually enter torpor (Kissner and Brigham, in press).

We collected these data in June–August 1991 and May–June 1992 in the Okanagan valley near Oliver, British Columbia (49°18′N, 119°31′W) and July–August 1992 in the Cypress Hills, 60 km south of Maple Creek, SK (49°34′N, 109°53′W). We measured the activity of 11 different adult birds (9 males and 2 females, mean mass 49 g) using a Merlin 24 telemetry receiver (Custom Electronics, Urbana, IL) and 5-element Yagi antennae. Radio transmitters (model PD-2T, Holohil Systems Ltd., Woodlawn, Ontario) were affixed in a backpack with an elastic harness (Brigham 1992). The transmitter package weighed 2.4 g, which represents <5% of the bird's mass. Birds carrying transmitters acquired mates, nested normally, and appeared to forage normally by sallying from the ground. The behavior of each bird was classified as active or stationary every 5 min for 2 h after foraging began (approximately sunset) and for 2 h before foraging ended (approximately sunrise). During each 5-min interval, we monitored 20 pulses and assumed that any change in signal direction or strength reflected movement. Direct observations of birds feeding during twilight confirmed that the "movements" inferred by telemetry were actually foraging sallies (Brigham and Barclay 1992).

Telemetric measurements of poorwill activity were made on the two nights prior to the DLW protocol being undertaken and on the two nights following for six different birds on one occasion each. We divided the night into three time periods with different solar and lunar influence on light levels and poorwill activity (Brigham and Barclay 1992). We defined dusk as the period of nautical twilight after the sun sets until it is 12° (generally about 1 h; Anawalt and Boksenberg 1987) below the western horizon; dawn is defined as the period of nautical twilight before sunrise beginning when the sun is 12° below the eastern horizon (approximately 1 h before sunrise); and "true night" is the period between dawn and dusk

when the sun is >12° below either horizon. Thus, on any given night, we assessed poorwill activity for all of the dusk and dawn periods and approximately 2 h of the true night period.

The DLW protocol or sham treatments (see below) were always applied between 06:00 and 10:00 h CST after night 2. Birds were flushed into a mist net and then injected with 150–170 ml of $^3H_2O^{18}$ intra-peritoneally using a 10-mm needle. The bird was weighed and then held in a cloth bag for one hour to allow the isotopes to equilibrate with body fluids. Microcapillary tubes were used to collect a blood sample (50–150 ml) after brachial vein puncture. In almost every instance, a small hematoma formed after the bleeding stopped. Two sham experiments were also conducted. First, three different birds were flushed off a nest on the ground three times in 30 min but not captured or injected. This procedure was the same used when we were attempting to capture birds for injection or blood sampling. The second sham experiment involved two different birds who were caught, weighed, held for one hour and had a blood sample taken, but no injection was administered. The sham experiments were conducted as a control for the effects of handling stress and the injection itself on behavior. For both sham experiments, foraging activity was monitored in precisely the same way as for the experimental birds.

For each of the four nights that activity was monitored, we generated activity scores (percentage of measurements that were classified as moves) and assigned them to one of the three time categories (dusk, dawn, or true night). Scores were arcsin transformed before analysis. Although we found significant heterogeneity of variance using Bartlett's test (Zar 1984), we used a parametric two-tailed ANOVA to minimize the chance of a type II error (accepting the null hypothesis when it is actually false).

Of the eight birds subjected to the full DLW protocol (capture, injection, equilibration, and blood sample), two left the study area shortly after release. There was nothing clearly different in our application of, or the birds' direct response to, the protocol for these two individuals. For the six birds that remained, we found no significant difference in foraging activity before and after the protocol for any of the three time periods (dusk: $F = 2.00$, df $= 23$, $P > 0.10$; night: $F = 1.00$, df $= 23$, $P > 0.40$; and dawn: $F = 0.43$, df $= 23$, $P > 0.70$; Fig. 1). Likewise, for the five birds involved in sham experiments, there were no significant differences in activity scores (dusk: $F = 0.93$, df $= 19$, $P > 0.30$; night: $F = 0.37$, df $= 19$, $P > 0.50$; and dawn: $F = 1.16$, df $= 11$, $P > 0.20$). When the data for the six experimental and five sham birds were pooled, there were no differences in activity scores for the three time periods (dusk: $F = 1.08$, df $= 43$, $P > 0.30$; night: $F = 0.98$, df $= 43$, $P > 0.40$; and dawn: $F = 0.38$, df $= 33$, $P > 0.60$).

One of the two individuals that left the study area after the DLW protocol abandoned its nest but returned to the study area subsequent to the monitoring period. The second bird, which was not nesting at the time, also left the study area during our two-day monitoring period. The mate of this bird, caught and treated on the same day, remained in the same area for the rest of the summer. On at least six other occasions during 1991, tagged poorwills left the study area for short periods (1–3 days). These departures were not associated directly with disturbance due to capture attempts.

For the DLW technique to be a valid means of measuring FMR, it is essential that the procedure have minimal effects on the activity patterns of the study animal. If activity changes significantly as a result of the DLW protocol, an accurate measurement of energy expenditure may not reflect the actual amount of energy expended by an animal that is behaving normally. Our results support the conclusions of two other studies which report negligible effects of the DLW protocol, at least for the birds that remained in the study area. Bryant and Westerterp (1983) found that the energy expenditure by a single injected House Martin (*Delichon urbica*) differed from that of a control bird by only 2%. In a larger study, Speakman et al. (1991) found no discernable effect on the behavior of laboratory

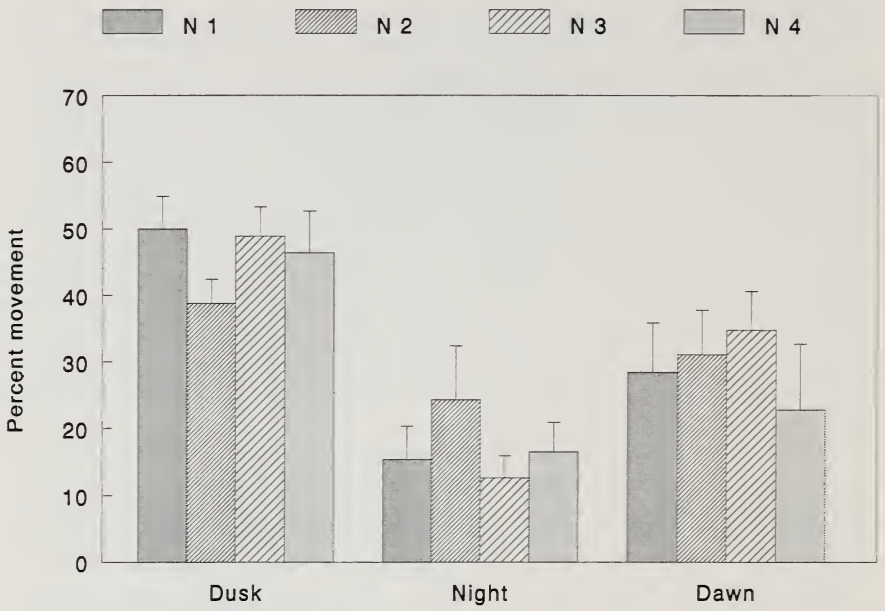

FIG. 1. Histogram (mean ± SE) of untransformed activity scores for dusk, night and dawn for six birds treated with the DLW protocol. Nights 1 (N1) and 2 (N2) occurred before the protocol was applied, nights 3 (N3) and 4 (N4) after the protocol was applied.

white mice (*Mus musculus*), although they conceded that the effect could have been masked by the stable laboratory conditions and the fact that they used domesticated animals. Our work extends that of Speakman et al. (1991) by suggesting that the DLW technique has a negligible effect on free-ranging poorwills that remain in the study area, although different species may be more or less sensitive to the disturbance caused by handling.

Because two birds left our study area after being injected, it is important for the DLW protocol to monitor the free-ranging organisms under study to confirm that "normal" behavior is not dramatically altered. Our manipulations appear to have had an all-or-none effect in that birds either behaved normally or left the study area. It was not uncommon for non-experimental birds to leave the study area for brief periods. These brief departures could not be ascribed to a clear cause and thus may represent a normal behavior (e.g., foraging, mate acquisition). Obviously, more studies to assess the impact of the DLW protocol on other free-ranging animals are required to establish the generality of our results.

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Wilson Bull., 106(2), 1994, p. 416

Common snapping turtle eats duck eggs.—In the present note we report observations of a common snapping turtle (*Chelydra serpentina*) predating duck eggs. This behavior apparently has not been mentioned previously in the literature, although predation of ducklings by snapping turtles may be common (Babcock 1919, Carr 1952).

On 10 May 1993 while photographing ducks at Three Lakes Park in western Henrico County, Virginia, we observed a common snapping turtle taking individual eggs from several duck nests. The turtle was first observed at approximately 20:10 DST. It came out of a 1-ha pond onto a small island (9 × 10 m) on which Mallards and domestic ducks (*Anas platyrhynchos*) and Muscovies (*Cairina moschata*), were nesting. As it approached the nests, all of the ducks left the island except for one domestic duck which stood by her nest. The turtle went to this nest and removed a single egg, carrying it whole in its mouth back to the water. The turtle disappeared from view underwater, but returned to the island several minutes later. We did not see it eating the eggs, but each egg was well within the turtle's mouth when last seen. This process was repeated at least four times before it became too dark to see the island. The site was checked the next day and all of the nests were empty and abandoned. Mallards nested again on the island three weeks later, but these nests were abandoned within a week. It appeared that only a single large turtle was involved. Its carapace length was estimated from photographs to be 30–40 cm.

While predation of a wide variety of live animals by common snapping turtles has been documented, no previous reports of turtles eating bird eggs are known to us (Alexander 1943, Lagler 1943, Carr 1952, Ernst and Barbour 1977). If turtles are capable of learning to recognize eggs as food, their predation of nests could become an important source of nest failure for waterfowl.

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ORNITHOLOGICAL LITERATURE

CURRENT ORNITHOLOGY. Volume 10. Edited by Dennis M. Power. Plenum Press, New York. 1993: xiv + 383 pp. $85.00 (cloth).—This review series has now spanned a decade, a tribute to the importance of the service it provides. The present volume deals with subjects as diverse as "trophic structure of raptor communities: a three-continent comparison and synthesis" and "evolution of avian ontogenies."

The first paper in the volume, "The role of phylogenetic history in the evolution of contemporary avian mating and parental care systems," by J. D. Ligon, is a rich, imaginative review of mating systems. I intend to assign it as required reading to bird students, once they have sufficient taxonomic background to follow the phylogeny.

"Trophic structure of raptor communities: a three-continent comparison and synthesis," by C. D. Marti, E. Korpimaki, and F. M. Jaksic, is unusual in that it is more of an analysis of existing data than a review of existing literature, although the literature review is also extensive, and the paper is a wonderful source of citations and sources for raptor diet data.

"Matrix methods for avian demography," by D. B. McDonald and H. Caswell, is, at first, daunting to those of us with a phobia for equations and symbols. However, the problem is illusionary. The text, while dealing with complex analyses, is readable and the symbolism clear and easily (even by me) followed. The paper will undoubtedly be useful to students of avian populations, a research area which becomes more important with growth of human populations.

"Nocturnality in colonial waterbirds: occurrence, special adaptations, and suspect benefits," by R. McNeil, P. Drapeau, and R. Pierotti, amazed me in its content. I simply had no idea that so much work had been done in the field. Reading this chapter led me to add a lot of material on the subject to my class lectures on avian behavior.

"Latitudinal gradients in avian species diversity and the role of long-distance migration," by K. N. Rabenold, is the shortest chapter in the volume. This may be a result of the existence of previous reviews of materials related to the topic. Understanding evolutionary and ecological control of species diversity has been one of the major thrusts of ornithology over the past three decades. Rabenold's chapter carries this subject forward significantly without being redundant.

"Evolution of avian ontogenies," by J. M. Starck, is very different from other chapters in the volume. Profusely illustrated, it covers growth and development from the perspective of histology, embryology, morphology, and ecology. It truly is a synthesis of ornithological ontogeny.

It is obvious that reviews in this series have become much more specialized (and their titles longer) in comparison with earlier issues. (First volume titles such as "Comparative avian demography" and "Bird chromosomes" were typical of earlier volumes.) This, perhaps, is a consequence of the considerable growth and development of information about ornithological subject materials. It has always been my contention that ornithology is first of all a science like all other branches of zoology. It therefore should be expected that knowledge in the field should become more fine-structured, technical, and insightful.

The present volume accomplishes what I expect from a review series. The papers thoroughly review their subject materials, survey the most modern advances, and synthesize the findings in a way that extends our understanding a bit farther.—C. R. BLEM.

THE BIRDS OF CAPE MAY. By David Sibley. New Jersey Audubon Society, Franklin Lakes, New Jersey, 1993: 150 pp. Price not known. (paper).—This guide will be very useful to birders visiting Cape May, and according to the foreword in the book, more than 100,000 birders visit the cape annually. The book essentially is an annotated checklist based mostly on data collected from 1985–1992. Each species that has been recorded at Cape May is given paragraph coverage including habitat preferences, local variation in status, daily maxima, year-to-year fluctuations, historical changes, and other information. The standard bar graphs designating abundances are included. The book was produced entirely by desktop publishing and was printed locally. Hopefully this reduces costs, but the book is attractive, clearly written, and thorough. The book will be available only through New Jersey Audubon Society centers (including the Cape May Bird Observatory, P.O. Box 3, Cape May Point, New Jersey 08212) until late summer 1994, when it will be available to commercial distributors. Get a copy of this manual plus a Cape May County, New Jersey, map and you will be ready to get a full appreciation of one of the most historic birding areas in the eastern United States.—C. R. BLEM.

THE BIRDS OF CITES AND HOW TO IDENTIFY THEM. By Johannes Erritzoe. Illustrated by Helga Boullet Erritzoe and the author. The Lutterworth Press, Cambridge, U.K. 1993: xxii + 198 pp., 75 color plates, 10 black-&-white plates. $161 (leatherbound), $51 (hard back), $44 (ringbound).—The Convention on International Trade in Endangered Species (CITES) has listed 1478 species and subspecies of birds that are of concern. The present volume attempts to provide a guide to the identification of these species for the use of all those who might have to deal with the provisions of the Convention (i.e., importers, aviculturists, customs officials). It describes and illustrates in color 406 of these species. Included are all those on CITES List I, II, and III except for those "look-alike" species (e.g., 269 birds of prey) not on List I. The "look-alike" species are listed and a black-and-white figure is given for each genus.

The text for each species is minimal and gives the name in English, German, French, and often Spanish or Portuguese; a brief statement of range; details of description, a terse statement of Status, including population estimates for List I species, and several literature references. The introduction supplies an illustrated guide to the bird families. An appendix gives the full text of the Convention and a useful glossary giving the French, German, and Spanish translations of the English terms used in the text.

The paintings of the birds are attractive. Although not of world class, they will serve adequately for identification purposes.—GEORGE A. HALL.

DUCKS IN THE WILD. Conserving Waterfowl and their Habitats. By Paul A. Johnsgard. Prentice Hall, New York, New York. 1992: 160 pp., 130 color photographs and illustrations; 20 line drawings; maps. $30.—After writing of many bird families the prolific Paul Johnsgard has returned to his first love—waterfowl. The result is this attractive volume which is more than the coffee table book the format suggests. As might be expected, Johnsgard writes with skill and feeling and has produced a worthwhile non-technical treatment of the ducks of the world.

The main text is a species by species account of 113 duck species, divided into ten tribes. Each species account is accompanied by an excellent color photograph and a small map of the breeding range. For a few species for which no photographs are available, a painting is

given. Most accounts occupy a full page but some of the less well-known species are given only a half page. These accounts concentrate on life history characteristics, but occasionally discuss such things as a classification, identification marks, and conservation matters.

The leading chapter, "The Magic of Waterfowl" is an eloquent invocation to waterfowl, and a chapter, "Watching Waterfowl," suggests things the reader should observe in the field. A chapter entitled "Extinct and Endangered Ducks" discusses the four species that have become extinct in historical times: Crested Shelduck (*Tadorna cristata*); Labrador Duck (*Camptorhynchus labrodorius*); Pink-headed Duck (*Rhodonessa caryophyllacea*); and Auckland Islands Merganser (*Mergus australis*), and gives a list of 14 full species and 11 subspecies that are considered endangered. This chapter also has a long treatment of waterfowl and wetland conservation, particularly in North America. There is an underlying theme of conservation throughout the book.

The book closes with an illustrated identification key to 106 of the species treated, a glossary of terms and a brief selected bibliography.

The book is highly recommended for the general reader interested in waterfowl, and the collection of photographs will be of interest to many ornithologists.—George A. Hall.

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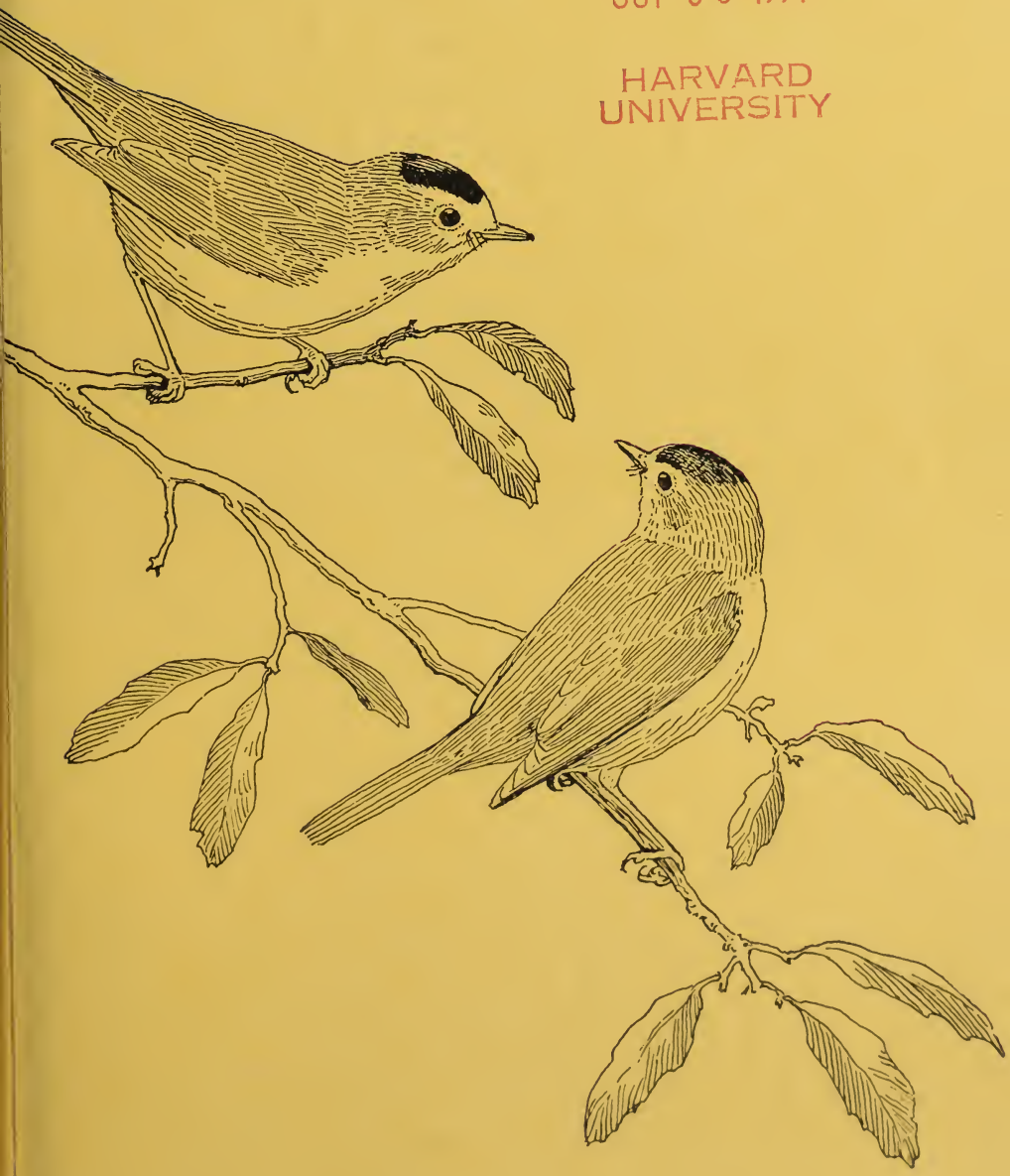

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Family group of ʻAkiapolaʻau feeding in koa (*Acacia koa*) and alani (*Melicope* sp.): uppermost, male in subadult plumage; lower left, juvenile; center, adult male; lower right, adult female. Watercolor painting by H. Douglas Pratt.

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IDENTIFYING SEX AND AGE OF AKIAPOLAAU

THANE K. PRATT, STEVEN G. FANCY, CALVIN K. HARADA, GERALD D. LINDSEY, AND JAMES D. JACOBI

ABSTRACT.—Methods for identifying the sex and age of the Akiapolaau (*Hemignathus munroi*), an endangered honeycreeper found only on the island of Hawaii, were developed by examination and measurement of 73 museum specimens and 24 live birds captured in mist nests. Akiapolaau probably undergo a single annual molt, with most birds molting between February and July. The mottled juvenal plumage is replaced by a first basic plumage characterized by yellowish-gray or yellowish-green underparts and often by retained wingbars. Male Akiapolaau may not attain adult plumage until their third molt. In adult females, only the throat and upper breast become yellow, whereas in adult males the superciliaries, cheeks, and entire underparts are yellow. Adult males have greater exposed culmen, gonys, wing chord, tail, and tarsus lengths than do females. Akiapolaau in first prebasic molt or older can be identified as to sex by culmen length, that of males being >23.4 mm. *Received 19 Aug. 1993, accepted 1 Dec. 1993.*

The Akiapolaau (*Hemignathus munroi*) is an endangered Hawaiian honeycreeper (Fringillidae: Drepanidinae) best known for its dual-action beak in which the mandible is a stout awl and the maxilla an elongated hook (Frontispiece). The species is distributed patchily through montane mesic and dry forest on the island of Hawaii, where Scott et al. (1986) estimated 1500 birds in low population density. This study describes the plumage sequence and morphometric and plumage characters for identifying the sex and age of Akiapolaau, based on museum skins and on live birds captured in mist nets. Previous descriptions of plumage and measurements from museum specimens are brief and incomplete (Wilson and Evans 1890–1899, Rothschild 1893–1900, Henshaw 1902, Amadon 1950), and recently published illustrations only show adult males with accuracy.

National Biological Survey, Hawaii Field Station, P.O. Box 44, Hawaii National Park, Hawaii 96718.

METHODS

We recorded plumage characteristics and external measurements for 73 Akiapolaau skins at the Bernice P. Bishop Museum (BPBM), Honolulu, Hawaii, and the National Museum of Natural History (NMNH) in Washington, D.C. Fifty-two of these specimens were collected by Henshaw (1902) between Hilo and Volcano from 1899 to 1902, a series never described in detail. Our sample included 64 specimens with sex indicated on the label. We assumed that birds were correctly sexed by examination of their gonads during specimen preparation. T. Pratt measured BPBM specimens and Kanakaleonui birds (see below); Michelle Reynolds, trained by Pratt, measured NMNH specimens. An additional 38 captures of Akiapolaau were measured, scored for molt, banded, and released where captured at Kulani Correctional Facility (C. Atkinson and R. Dusek, unpubl. data) or at Puu Laau and Kanakaleonui by various individuals (Fig. 1). Our analysis of timing of molt also included data for 57 captures of Akiapolaau at Keauhou Ranch (C. J. Ralph, unpubl. data).

We scored individual primaries, secondaries, and rectrices as missing, in sheath, or fully grown. All remaining feathers were considered body feathers and scored as (0) no molt, (1) 1–5 feathers in sheath, or (2) >5 feathers in sheath. Comparative wear on wing feathers of molting birds helped in determining which feathers were new or old. We considered birds to be in annual molt if more than five body feathers were in sheath or if primary and secondary feathers were molting symmetrically. We omitted juveniles from molt analysis because they do not undergo wing or tail molt.

For each specimen, we recorded the presence or absence of mottling on the head, throat, and upper neck, mottling being feathers tipped with darker gray in contrast to basal yellowish grey. We recorded presence or absence of wingbars (paler tips on greater and sometimes middle wing coverts). A ventral color score was assigned for each bird as follows: (1) all gray; (2) all yellowish gray or yellowish green; (3) chin and throat yellow, breast yellowish gray; (4) entirely yellow, cheeks green; or (5) entirely yellow, cheeks yellow. We coded the coloration of the superciliary as green or yellow and the coloration at the base of the mandible as pale or dark.

For each specimen, we also recorded standard measurements of wing cord (WING), exposed culmen (EXPCUL), tarso-metatarsus (TARSUS), and TAIL as described in Pyle et al. (1987) and Fancy et al. (1993). GONYS was measured from the tip of the mandible to the point where the rami join to form the gonys. We did not measure damaged structures.

After inspecting the frequency distribution of plumage and soft part scores and studying transitional plumages of birds in molt (see Results), we aged each specimen as juvenile, subadult, or adult. We conducted separate analyses for subadults and adults, using logistic regression and stepwise discriminant analyses to determine the best set of measurements for sexing Akiapolaau, and classified each museum specimen as to sex, using linear discriminant functions (SAS 1987). To produce unbiased error rates, we classified individuals by a jackknife procedure (i.e., each discriminant function was computed from the other observations in the data set, excluding the observation being classified; SAS 1987). The discriminant function was used to identify the sex of live birds that were independently sexed on the basis of plumage (adult males), breeding behavior, or presence of a brood patch (National Biological Survey, unpubl. data).

We compared WING and EXPCUL measurements for adult male Akiapolaau at four sites to test for geographic variation in measurements. For other sex and age classes, too few specimens were available. Measurements were recorded for museum specimens from Kaiwiki (N = 10, 500–800 m elevation), Olaa (N = 9, 500–800 m), and Kilauea (N = 6, 1200–2000 m) and for eight live males captured in mist nets at Kanakaleonui (2400–2700 m, Fig. 2).

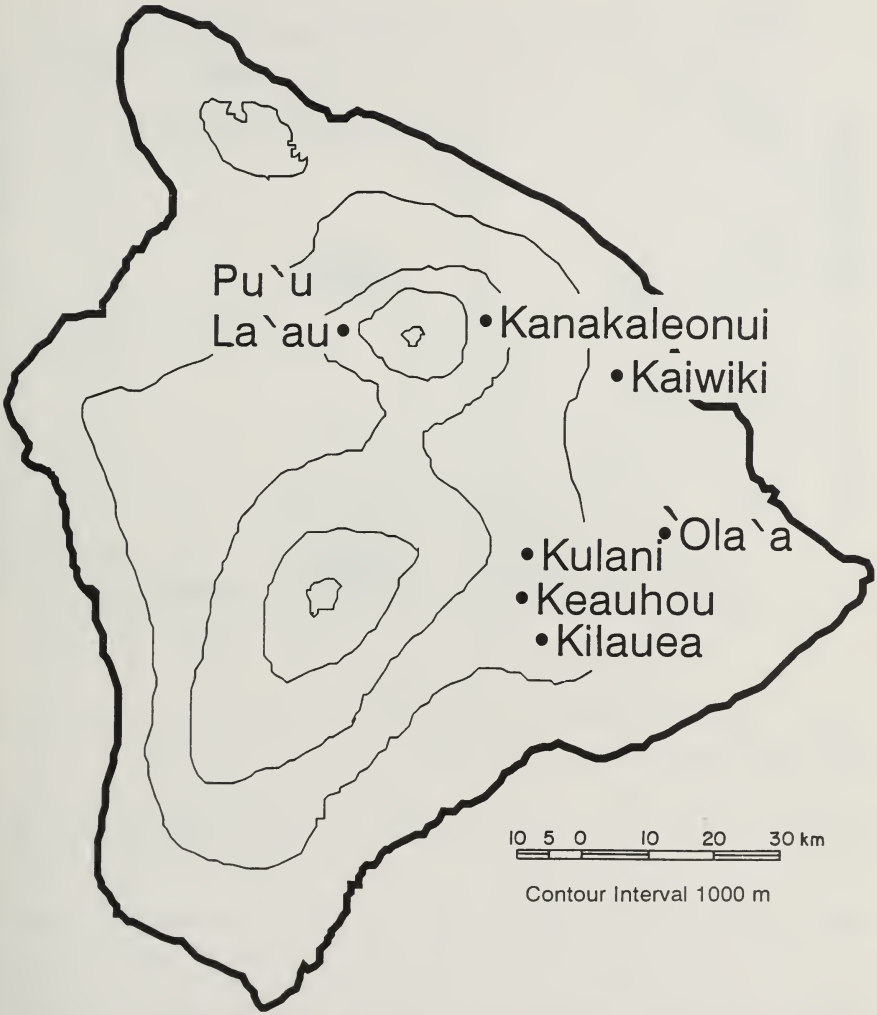

FIG. 1. Map of the island of Hawaii showing collecting and banding locations.

RESULTS

Seasonality of molt.—Though molting Akiapolaau have been captured throughout the year, our limited sample indicates a single broad peak in molting between February and July (Fig. 2). Absence of bimodal peaks suggests that the species molts once annually, as do other Drepanidinae (Amadon 1950, Baldwin 1953, Jeffrey et al. 1993).

Age identification.—The juvenal plumage of Akiapolaau, described

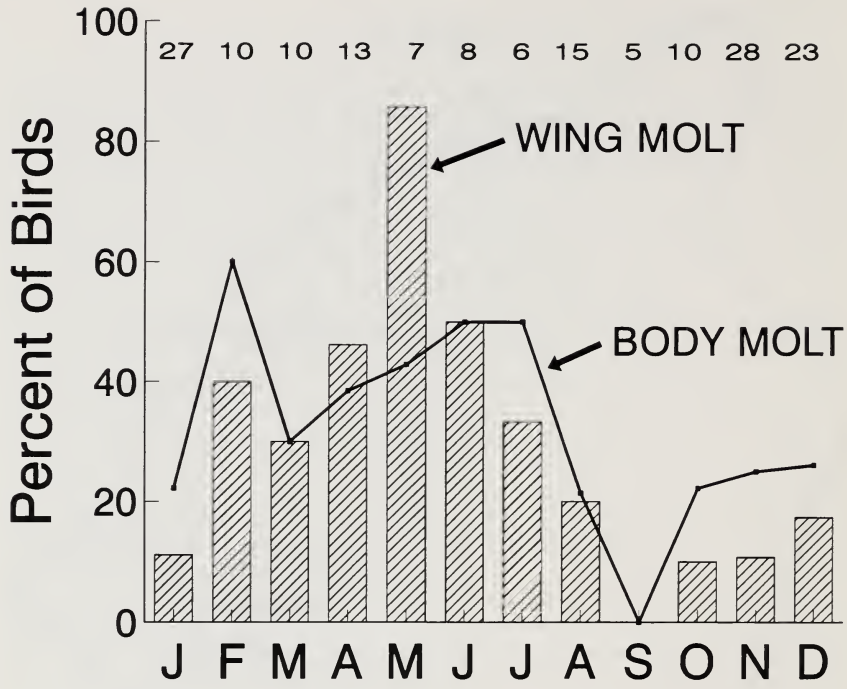

FIG. 2. Timing of wing (primary and secondary) and body molt in post-juvenile Akiapolaau. Sample sizes appear at top of the figure.

here for the first time, is characterized by a mottled appearance caused by dark-gray tips on the feathers of the head, throat, and upper breast. The plumage, overall, is yellowish-gray or green, with underparts paler (ventral score 2). Faint wingbars result from the thin, pale tips of greater and middle wing coverts. The mandible is yellowish at fledging but darkens to brown or black over a period of months, retaining pale coloration last at its base (Pratt, unpubl. data). Four specimens showed nearly complete juvenal plumage, and all were molting (body molt score 1 or 2 but no primary or secondary molt), suggesting that Akiapolaau begin their incomplete first prebasic molt within a few months of fledging.

The distinctive subadult plumage resembles juvenal plumage but lacks mottling. The underparts are pale yellowish gray or yellowish-green (ventral score 2), although a few females had grayish plumage with very little yellow suffusion (ventral score 1). Thirteen specimens had wingbars on the retained juvenal wing coverts (Fig. 3). Five specimens lacked wingbars that may have been too vague to be recognized, had worn off, or may have molted during the first prebasic molt. Presence of wingbars is

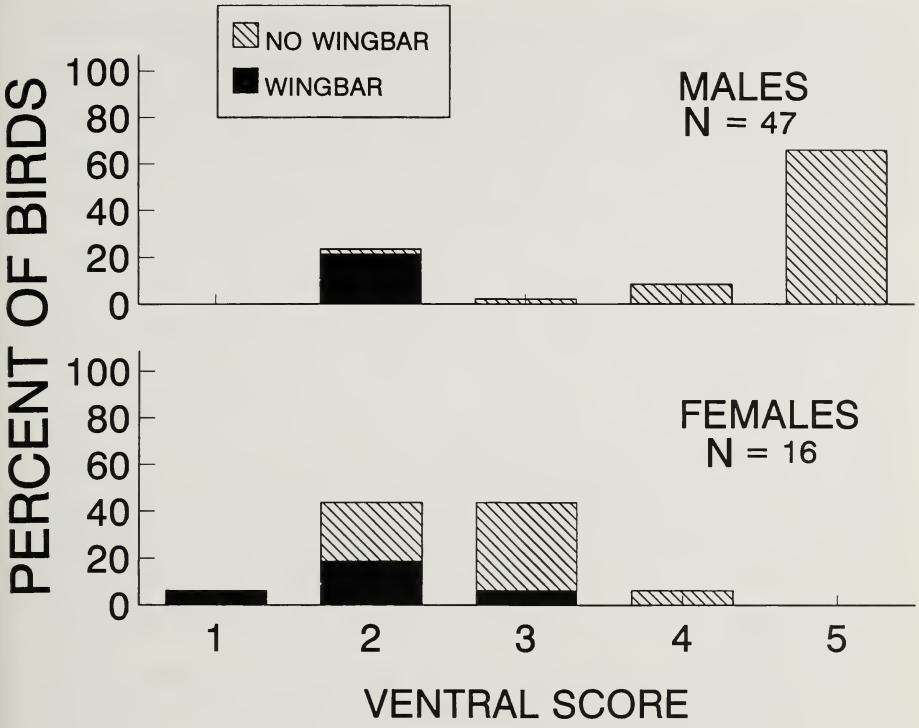

FIG. 3. Distribution of plumage scores for male and female Akiapolaau museum specimens. Ventral score is coded as (1) all gray, (2) all yellowish-gray or yellowish green, (3) chin and throat yellow, breast yellowish-gray, (4) entirely yellow, cheeks green, or (5) entirely yellow, cheeks yellow.

useful for identifying birds as juveniles or subadults, but absence of wingbars should not exclude assigning a bird to these age classes. The mandible of subadults is dark; the base of the mandible was pale on only one of 18 specimens. Adult plumage follows the complete second prebasic molt: of eight subadults in annual molt, six were molting primary or secondary feathers symmetrically.

Adult females have a yellow chin, throat and upper breast that contrasts with a pale yellowish-gray lower breast and belly (ventral score 3). This plumage lacks wingbars, although one adult female specimen retained wingbars (Fig. 3). One male specimen, without wingbars, possessed this plumage and may have been a subadult. We do not know if some females retain ventral score 2 for more than one year. One female had entirely yellow underparts and green cheeks (ventral score 4) and lacked wingbars and may have been in her second or later basic plumage.

Adult males have yellow superciliaries, cheeks, and underparts (ventral score 5), no wingbars, and black rather than dark gray lores. Four male specimens had yellow underparts and green cheeks (ventral score 4), no wingbars, and greenish superciliaries. One was molting from ventral score 2; another was molting into ventral score 5 (Fig. 3). Of these four birds, two with new flight feathers appeared to have undergone complete molt and may have been in their second or third basic plumage.

Recaptures and sightings of banded birds showed that the adult plumages for males and females did not change between molts. We captured one female in subadult plumage (ventral score 2) that when captured eight months later had molted into adult plumage (ventral score 3) and was tending a fledged chick. A captured female with gray plumage and a wingbar had an active brood patch (Lepson, pers. comm.), indicating that females in subadult plumage can breed.

We were unable to age birds reliably from measurements alone. Subadult and adult females differed only in wing chord length, which was shorter in subadults ($t = 2.14$, 14 df, $P = 0.051$). Subadult males had shorter WING ($t = 2.30$, 40 df, $P = 0.026$), EXPCUL ($t = 2.41$, 30 df, $P = 0.022$) and GONYS ($t = 2.70$, 37 df, $P = 0.011$) measurements than did adult males.

Sex identification.—Only adult male Akiapolaau can be sexed reliably by plumage characteristics, so we conducted separate analyses for subadult and adult Akiapolaau to develop criteria for sexing birds from measurements. EXPCUL was the only variable to enter the discriminant function for sexing subadult birds. We accurately sexed 17 of 18 (94%) subadults by identifying all birds with EXPCUL lengths ≥23.3 mm as males and those with shorter culmens as females. In separate *t*-tests, subadult males had longer wing, exposed culmen, gonys, and tarsus lengths than did subadult females (Table 1).

The discriminant function:

$$D = 1.318(\text{EXPCUL}) + 0.313(\text{WING}) - 55.689$$

correctly sexed 28 of 30 (93%) adult Akiapolaau, in which birds with a discriminant score of $D \geq 0$ are identified as males. Adult male Akiapolaau had longer wing, culmen, and gonys lengths than did adult females (Table 1).

We also computed a discriminant function after pooling data for subadult and adult Akiapolaau because of the difficulty in identifying the age of some postjuvenile birds. We accurately sexed 44 of 48 (92%) subadult and adult museum specimens by identifying all birds with EXPCUL ≥23.4 mm as males and those with smaller culmens as females. We also found that a cutoff EXPCUL length of 23.4 mm accurately sexed 37 of

TABLE 1

COMPARISON OF MEASUREMENTS (MM) FOR MALE AND FEMALE AKIAPOLAAU SPECIMENS BY AGE CLASS

	Females				Males					
	N	Mean	SE	Range	N	Mean	SE	Range	t^a	*P*
Juvenile										
Wing chord					5	79.00	0.95	76.0–81.0		
Tail					5	41.80	0.86	39.0–44.0		
Exposed culmen					4	24.57	1.11	22.5–27.7		
Gonys					5	13.50	0.45	12.3–14.7		
Tarsus					5	24.94	0.26	24.3–25.5		
Subadults										
Wing	10	77.30	0.42	75.0–80.0	10	79.70	0.73	77.0–85.0	2.8	0.011
Tail	10	41.40	0.43	39.0–43.0	10	43.20	0.90	40.0–48.0	1.8	0.095
Exposed culmen	10	21.45	0.34	19.6–23.1	8	24.96	0.47	23.3–26.9	6.2	0.000
Gonys	10	11.93	0.18	10.9–12.6	10	13.10	0.25	12.2–14.7	3.8	0.001
Tarsus	9	24.36	0.22	23.0–25.1	9	25.10	0.26	23.8–26.1	2.2	0.044
Adults										
Wing	6	78.67	0.42	77.0–80.0	32	81.56	0.39	77.0–88.0	3.1	0.004
Tail	6	42.50	0.56	40.0–44.0	32	43.88	0.36	40.0–49.0	1.6	0.119
Exposed culmen	6	21.97	0.80	19.4–24.8	24	26.61	0.36	22.6–30.8	5.6	0.000
Gonys	5	11.88	0.45	11.0–13.4	29	13.87	0.14	12.6–15.6	5.1	0.000
Tarsus	6	24.03	0.42	22.7–25.3	31	25.06	0.17	23.4–28.0	2.5	0.019

[a] *t*-test for difference in measurements between sexes.

38 (97%) live birds (including recaptures) from an independent sample of 17 adult males and six subadult and adult females. One female from Kanakaleonui had an EXPCUL of 23.9 mm.

Geographic variation in measurements.—Skin specimens from Kai-

TABLE 2

WING AND EXPOSED CULMEN MEASUREMENTS (MM) FOR ADULT MALE AKIAPOLAAU AT FOUR SITES

		Wing			Exposed culmen		
Site[a]	Elevation (m)	N	Mean	SE	N	Mean	SE
Kaiwiki	500–800	10	81.4	0.60 (A)[b]	8	26.6	0.37
Olaa	500–800	9	81.7	1.05	6	28.2	0.64 (A)
Kilauea	1200–2000	6	82.2	0.40	5	25.3	0.77 (A)
Kanakaleonui	2400–2700	8	84.4	0.65 (A)	8	27.5	0.55

[a] Birds from Kanakaleonui were measured alive; all others were museum skins.

[b] Means with the same letter are significantly different ($P < 0.05$, Tukey's studentized range test, SAS 1987).

wiki had shorter wings than live adult males at Kanakaleonui (Table 2). Exposed culmen lengths of Kaiwiki and Kanakaleonui males did not differ significantly from culmens of males from other sites, but skins of males from Kilauea had significantly shorter culmens than those from Olaa (Table 2).

DISCUSSION

Akiapolaau can breed and molt at any time of year (Amadon 1950; Banko and Williams 1993; Ralph and Fancy 1994; this study) and so cannot be aged by the calendar year method of the USFWS Bird Banding Laboratory (Canadian Wildlife Service 1984). Phenology of breeding is not well understood. Banko and Williams (1993) summarized data for five Akiapolaau nests discovered in January (2 nests), February, July, and October. Lepson (pers. comm.) reported three active nests in March, May, and June. Ralph and Fancy (1994) captured males with enlarged cloacal protuberances throughout the year and captured females with brood patches in January, February, May, June, August, and October. Atkinson and Dusek (unpubl. data) captured females with brood patches in March and June. These few data suggest that most Akiapolaau nest from January through August.

In passerines, annual molt generally follows breeding (Newton 1972, King 1974, Pyle et al. 1987). Amadon (1950) reported molt in Akiapolaau from June through September. We found that although most Akiapolaau molt in spring and summer, birds in prebasic molt can be found at any time of year. Other native forest birds in Hawaii breed during spring and summer and molt in late summer and fall, with very few birds molting at other times (Amadon 1950; Fancy et al. 1993; Jeffrey et al. 1993; Ralph and Fancy 1994). Akiapolaau appear to be unique among Hawaiian forest birds in that seasonality in breeding and molting overlap and that in any month a larger proportion of Akiapolaau are molting. Perhaps individual Akiapolaau molt over a relatively long period. Alternatively, weak seasonality in breeding by Akiapolaau may result in weak synchrony in molt within the population. Further, Akiapolaau parents, unlike other drepanidines, provide care for juveniles for many months (Lepson, pers. comm.; Pratt, unpubl. data), which may prevent renesting but permit the early onset of molt. If so, the long period of molt may be due to renesting by some birds that postponed molt until young were successfully fledged from subsequent nests.

The mottled juvenal plumage of Akiapolaau may be homologous to the dark-tipped juvenal plumage of other drepanidines (e.g., Laysan and Nihoa finches [*Telespyza cantans* and *T. ultima*], Apapane [*Himatione sanguinea*], and Iiwi [*Vestiaria coccinea*]). Also in common with many

drepanidines, Akiapolaau begin their first prebasic molt within a few months of fledging and often retain the pale-tipped juvenal wingbars in the first basic plumage.

Akiapolaau show variation in first basic plumage for both sexes and possibly for later female plumages. Molt in some specimens suggests that males may undergo more than two prebasic molts to attain adult plumage, as in another drepanidine, the Akepa (*Loxops coccineus*; Freed et al. 1987; J. Lepson, pers. comm.). Additional field studies are needed to better understand variation in plumages and molt sequence of Akiapolaau.

Identifying the sex of Akiapolaau in juvenal plumage is difficult because of uncertainty about the month of hatching and because bill length, which we found to be the most useful means of sexing older birds from measurements, increases during the first year. We found no difference in bill measurements between subadult and adult females, indicating either that bill growth stops during the first year or that we misidentified some adults as subadults. Or perhaps in a larger sample size, we could have detected a difference. Adult males had longer EXPCUL and GONYS than did subadult males, however, indicating that in males the bill continues to grow into the birds' second year. Perhaps the foraging niche of males changes as they mature or bill length may serve as a secondary sexual character.

Akiapolaau measurements showed little geographic differentiation. The four sites sampled spanned 2100 m in elevation and included extremely wet lowland rainforest (Kaiwiki and Olaa), montane mesic forest (Kilauea), and subalpine xeric woodland (Kanakaleonui). Akiapolaau, being territorial and sedentary, would not be expected to move among these sites. WING averaged about 3% larger for birds from Kanakaleonui, the site of greatest elevation. This size difference may be an artifact of comparing measurements from live birds with those from study skins, which shrink in preparation (Herremans 1985). If not, then Akiapolaau support the trend in size increase with altitude for some nonmigratory tropical bird species (Diamond 1972). The three males that were incorrectly sexed by the discriminant function because of small EXPCUL were from Kilauea. These males had larger EXPCUL than females from that site. We recommend that persons using measurements to sex Akiapolaau be wary of potential regional differences. Nevertheless, sexes from a single site should be easily distinguished by measurements, and if necessary, an adjusted cutoff point can be established for a local population.

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POPULATION TRENDS OF SHOREBIRDS ON FALL MIGRATION IN EASTERN CANADA 1974–1991

R. I. G. Morrison, C. Downes, and B. Collins[1]

Abstract.—Analysis of data from the Maritimes Shorebird Survey, involving counts of shorebirds made during fall migration in the Atlantic Provinces of Canada, indicated declines in a number of shorebird populations during the period 1974–1991. Significant declines were recorded most consistently for Least Sandpiper (*Calidris minutilla*), Semipalmated Sandpiper (*C. pusilla*), and Short-billed Dowitcher (*Limnodromus griseus*), and decreases for Red Knot (*C. canutus*) and Black-bellied Plover (*Pluvialis squatarola*) approached statistical significance in some analyses. Population trends were not constant but varied consistently across species during different phases of the study period. Declines occurred in most of the 13 species analyzed during the latter part of the 1970s, followed by increases during the first half of the 1980s, with a less marked tendency towards declines in recent years. A series of cold summers on the breeding grounds during the 1970s may have led to the observed population declines at that time. Statistical power analysis indicated that population changes of 2–5% should be detected at 80% power for the number of sites and years of coverage for which data were available. *Received 26 Aug. 1993, accepted 14 Dec. 1993.*

Many Nearctic shorebird populations undertake very long migrations, some species moving between breeding grounds in the Canadian Arctic and wintering areas near the southern tip of South America (Morrison 1984, Morrison and Ross 1989). Many species, especially those that depend on coastal wetlands, concentrate to a marked degree both during migration and on the wintering grounds, with large proportions of the population occurring at only a restricted number of sites (Morrison and Ross 1989, Morrison 1991). Shorebirds are particularly vulnerable to loss or degradation of habitat in such areas (Myers et al. 1987). Extensive loss of wetlands has occurred in North America during the past and present centuries (Senner and Howe 1984). Wetland habitats used by shorebirds elsewhere in the Western Hemisphere are also increasingly threatened by industrial and recreational developments (Bildstein et al. 1991).

Little information is available on how shorebird populations are being affected by such threats. Analysis of International Shorebird Survey data collected in the eastern United States between 1974 and 1982–83 indicated that three of the 12 species analyzed had declined significantly (Howe et al. 1989). Six of the remaining nine species showed declines which, although not statistically significant, were substantial in terms of annual (3–12%) or cumulative (up to 75%) changes. Declines in shorebird

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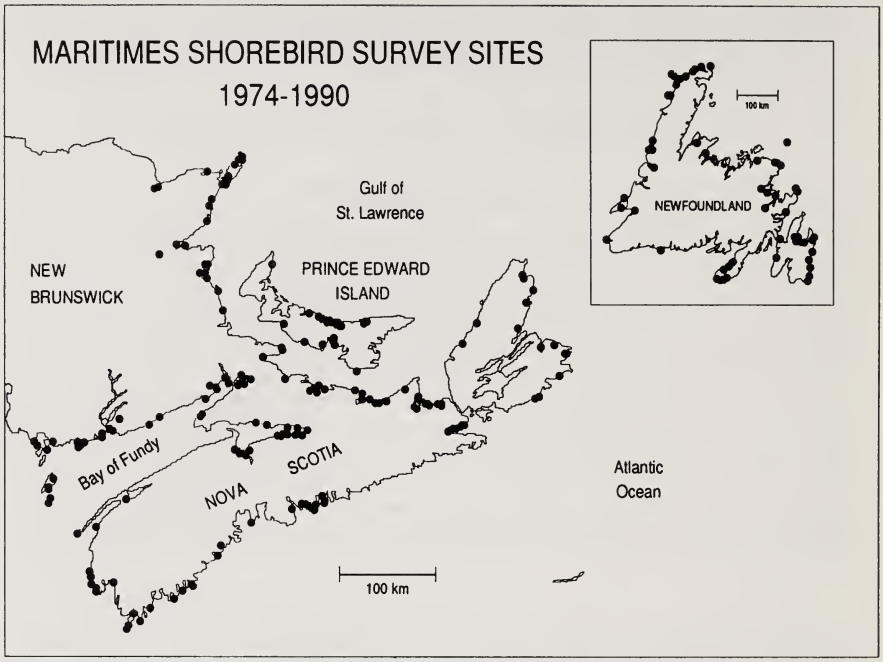

FIG. 1. Locations of sites surveyed during Maritimes Shorebird Survey operations 1974–1991.

numbers have also been suggested by data from James Bay, the St. Lawrence River system, and other parts of eastern Canada (Lariveé 1989, Morrison 1991, Morrison et al. 1991, Erskine et al. 1992).

The present paper uses data from the Maritimes Shorebird Survey to assess changes in numbers of shorebirds recorded on southward migration at sites in the Atlantic Provinces of Canada during the period 1974–1991.

METHODS

Field survey procedures.—The Maritimes Shorebird Survey (MSS) consists of a network of volunteers who count shorebirds at regular intervals at sites in the Atlantic Provinces of Canada (Fig. 1). Surveys during southward migration of shorebirds in the fall have been organized annually by the Canadian Wildlife Service since 1974. Sites in eastern and central U.S.A. and regions farther south are covered by the complementary International Shorebird Survey (ISS) organized by the Manomet Bird Observatory, Massachusetts. Although both schemes were designed to identify stopover areas and migration routes used by shorebirds, the data collected may also be used to examine trends in shorebird populations (Howe et al. 1989, Howe 1990).

Volunteers were provided with forms and detailed instructions to standardize survey protocols as much as possible. Participants were asked to adopt a clearly defined study area

TABLE 1

AVERAGE MAIN ADULT MIGRATION PERIODS FOR 13 SPECIES OF SHOREBIRDS IN ATLANTIC CANADA, 1974–1990

Species[a]	Main adult migration period
Black-bellied Plover (*Pluvialis squatarola*)	31 July–4 September
Lesser Golden-Plover (*P. dominica*)	26 July–30 August
Semipalmated Plover (*Charadrius semipalmatus*)	21 July–20 August
Willet (*Catoptrophorus semipalmatus*)	6 July–5 August
Whimbrel (*Numenius phaeopus*)	6 July–10 August
Ruddy Turnstone (*Arenaria interpres*)	21 July–18 August
Red Knot (*Calidris canutus*)	16 July–15 August
Sanderling (*C. alba*)	21 July–20 August
Semipalmated Sandpiper (*C. pusilla*)	16 July–15 August
Least Sandpiper (*C. minutilla*)	6 July–15 August
White-rumped Sandpiper (*C. fuscicollis*)	10 August–14 September
Dunlin (*C. alpina*)	9 Sept–9 October
Short-billed Dowitcher (*Limnodromus griseus*)	6 July–5 August

[a] Species identifications: It was not possible to check every bird in large flocks of Semipalmated Sandpipers. Such flocks may have contained a few small sandpipers of other species, but errors from this source were thought to be negligible. Long-billed Dowitchers are rare in the Atlantic Provinces and are not likely to have affected counts of Short-billed Dowitchers.

and to carry out counts in a consistent manner at the same stage of the tide on each survey. Surveys were conducted either at high tide, to count flocks of roosting shorebirds, or at intermediate tidal levels when shorebirds were concentrated on feeding areas. Counts were scheduled every second weekend from late July to late October to coordinate data collection. Participants were encouraged to conduct extra surveys. Direct counts were made wherever possible. Instruction sheets included suggestions for estimating numbers in large flocks (e.g., extrapolation from counting parts of flocks, estimation from size of flock and/or density of birds in flock). Emphasis was placed on obtaining reliable counts of the more common species of shorebirds. All observers were requested to provide basic information on survey conditions, species, and numbers and to record supplementary information on age and plumage of birds if possible. The latter information was used to determine migration phenology of adults and juveniles of each species and to associate age groups with peaks in counts.

Analytical procedures.—The 13 species of shorebirds selected for analysis (Table 1) were considered to have an ecological preference for coastal stopover sites with intertidal feeding areas rather than inland, freshwater habitats and thus likely to use MSS sites on a regular as opposed to opportunistic basis. Some 276 sites were censused during the period 1974–1991 (Fig. 1), although many received only limited coverage in terms of numbers of surveys or number of years of coverage. Effective sample sizes of sites available for population trend analyses for the different species generally fell in the range 30–80 (see Results).

For each species, the annual index used for investigating population trends of adults at each site was the mean number occurring during the main period of adult migration. Average main migration periods were determined for each species by calculating the mean number occurring at each site, and then overall, for each five-day period between 1 July and the end of the season. Many species showed two or more peaks. Field observations of age/plumage confirmed that the first peak normally consisted of adult birds. The main period of

adult migration was determined by visual inspection of the graphs. This period was defined as lying between the dates at which counts rose above or fell below 10–15% of the maximum count in the first peak. The annual index was the mean of all counts falling within the main migration period. Preliminary investigations showed that the mean count, rather than the maximum count, was the most suitable index for trend analysis. Occasional atypically high counts at a site, resulting perhaps from unusually higher numbers of birds occurring because of weather conditions, tended to distort results obtained using maximum count indices (unpubl. data).

Three techniques were used to assess changes in shorebird abundance, as follows:

(1) Route regression analysis. This method was developed by Geissler and Noon (1981) for analysis of data from the Canadian and U.S. Breeding Bird Surveys and has been adapted for analysis of shorebird counts made at migration areas (Howe et al. 1989; Howe 1990, present paper). Population trends are first estimated for individual sites through linear regression of log-transformed annual population indices. The overall trend is then calculated as a weighted average of the individual site trends. Log transformations produce a linear trend when a constant annual percentage change occurs in a population and also stabilize the variance of the slope estimates. For MSS analyses, annual population indices were log-transformed (natural log) after addition of a constant (0.23) to allow handling of zero counts, and trends for individual sites were calculated through linear regression. Two weighting procedures were applied to individual site trends before calculation of the overall mean trend for the species (Collins and Wendt 1989, Collins 1990). The first involved weighting solely by the precision of the slope estimate. The weighting factor in this case is inversely proportional to the square root of the variance of the estimate. This procedure downweights sites for which there is an imprecise slope estimate or which have only been covered for a limited number of years. The second procedure involved weighting by the product of the precision of the slope estimate and the mean (geometric) number of adult birds at the site. This method gives greatest weights to sites with large numbers of birds. The trend, or rate of change of the population, is defined as the slope of the linear regression line on the log scale; this may be back-transformed (Bradu and Mundlak 1970), or, since its value is not easy to intrepret biologically, may be presented, for instance, as half-lives, yearly, or 10-yearly rates of change (Collins 1990). There were few changes of observers at sites, and subsetting of routes for this reason was not considered necessary.

Trend analyses were also performed for the period 1974–1983 to enable a direct comparison to be made with the results reported by Howe et al. (1989) and for the subsets of years used in the paired *t*-test comparisons (see below).

(2) Theil's non-parametric trend test. Theil's estimate of the slope coefficient (Hollander and Wolfe 1973) is a non-parametric method which produces unbiased and robust estimates of the slope. Trend estimates for individual sites were combined to produce an overall estimate across all sites and significance levels computed through a randomization test based on 1000 permutations of the data. This procedure was applied to 15 sites which had received coverage in at least eight of the 17 years of surveys between 1974 and 1990.

(3) Paired *t*-test comparisons. Route regression methods assume a constant rate of change of population during the period of the survey. This assumption, however, is not likely to be met in practice. Changes in the mean abundance of each species at each site were investigated directly using a paired *t*-test procedure. The 18-year span of the study was divided into three equal time blocks: 1974–1979, 1980–1985, and 1986–1991. The annual index values for each site were averaged for each time block and compared using a paired *t*-test procedure.

Statistical significance and power analysis.—The significance level for statistical tests, also known as the Type I error rate, may be regarded as the probability of declaring that a

significant trend exists when there is no underlying trend in the population. Results are conventionally regarded as being statistically significant when this probability is less than 5%, i.e., $P < 0.05$. In the present work, the highly variable nature of the count data suggests that the 0.05% level of significance may be unduly restrictive, and we have adopted the convention of describing results where P is in the range 0.05–0.10 as being of "borderline significance".

The Type II error rate is the probability of declaring that there is no trend in the population when in fact a trend does exist. The statistical power of a test is defined as 1 minus the probability of a Type II error. Whereas one can control the critical value for the Type I error only using the sample size, the power of the test can be adjusted using both the sample size and magnitude of the effect that is being examined. The statistical power of the survey scheme will depend on two components making up the sample size, i.e., the number of sites being covered and the number of years which they are covered, as well as on the magnitude of the trend to be detected. Methods for calculating statistical power of Breeding Bird Surveys have been developed by Collins (1990) and adapted for shorebird surveys in the present work.

RESULTS

Migration phenology.—Main adult migration periods generally lasted 4–5 weeks (Table 1). About half of the 13 species occurred principally between mid-July and mid-August. Willets (see Table 1 for scientific names) and Short-billed Dowitchers migrated mostly in July, the two large plovers in August, White-rumped Sandpipers between mid-August and mid-September, and Dunlin, which complete a wing molt before moving south to the Atlantic coast (see Morrison 1984), not until September. The two-weekly sampling protocol usually resulted in three counts during the main adult migration period of most species at each site.

Route regression analysis.—Using slope precision × mean count weighting, route regression analysis showed that nine of the 13 species decreased between 1974 and 1991 (Table 2). Most (9 out of 13) of the calculated trends were less than 3%/year and were not statistically significant. Only the Least Sandpiper showed a statistically significant decline, although the large annual rate of decrease recorded for the Red Knot (−15.3%) was notable.

With slope-precision-only weighting, 10 of the 13 species showed negative trends (Table 3). This represented a significant tendency towards declines across species (Wilcoxon signed rank test, $P < 0.05$). The majority of calculated trends (8 out of 13) were again less than 3%/year and not statistically significant. The larger negative trends for Semipalmated Sandpipers, Least Sandpipers, and Short-billed Dowitchers were all statistically significant. A substantial, although not statistically significant, rate of decline (−5.24%/year) was again noted for Red Knots.

Trend estimates produced by the two weighting methods were generally

Table 2

Population Trends Calculated Using Route Regression Methods for Selected Shorebird Species during the Period 1974–1991[a]

Species	No. sites	Trend ± SE[b]	Annual change (%)	10-yr change (%)	Range of mean counts	*P*
Black-bellied Plover	85	−0.040 ± 0.039	−3.90	−32.8	0.2–278	0.32
Lesser Golden-Plover	27	−0.003 ± 0.016	−0.33	−3.24	0.2–1.4	0.84
Semipalmated Plover	82	+0.036 ± 0.049	+3.62	+42.7	0.4–623	0.47
Willet	38	−0.011 ± 0.024	−1.06	−10.1	0.3–55	0.66
Whimbrel	33	+0.007 ± 0.044	+0.74	+7.61	0.3–18	0.87
Ruddy Turnstone	66	+0.012 ± 0.025	+1.21	+12.7	0.3–39	0.63
Red Knot	37	−0.166 ± 0.132	−15.3	−80.9	0.3–26	0.22
Sanderling	50	−0.015 ± 0.039	−1.48	−13.9	0.2–380	0.70
Semipalmated Sandpiper	77	−0.011 ± 0.032	−1.10	−10.5	0.3–47,691	0.73
Least Sandpiper	71	−0.142 ± 0.061	−13.2	−75.8	0.3–153	0.02
White-rumped Sandpiper	57	−0.030 ± 0.038	−2.94	−25.8	0.3–203	0.44
Dunlin	40	−0.013 ± 0.031	−1.32	−12.4	0.3–53	0.68
Short-billed Dowitcher	55	+0.014 ± 0.056	+1.39	+14.9	0.3–73	0.81

[a] Based on mean counts during peak adult migration periods. Site weighting factors include precision of estimate and geometric mean of mean counts at site during survey period.
[b] Weighted mean slope on log scale.

Table 3

Weighted Population Trends Calculated Using Route Regression Methods for Selected Shorebird Species during the Period 1974–1991[a]

Species	No. sites	Trend ± SE[b]	Annual change (%)	10-yr change (%)	Range of mean counts	*P*
Black-bellied Plover	85	+0.009 ± 0.024	+0.90	+9.37	0.2–278	0.71
Lesser Golden-Plover	27	−0.006 ± 0.010	−0.63	−6.15	0.2–1.4	0.53
Semipalmated Plover	82	−0.028 ± 0.025	−2.76	−24.5	0.4–623	0.27
Willet	38	−0.0002 ± 0.027	−0.02	−0.18	0.3–55	0.99
Whimbrel	33	−0.001 ± 0.018	−0.12	−1.19	0.3–18	0.95
Ruddy Turnstone	66	+0.004 ± 0.023	+0.42	+4.30	0.3–39	0.86
Red Knot	37	−0.054 ± 0.044	−5.24	−41.6	0.3–26	0.23
Sanderling	50	−0.043 ± 0.026	−4.16	−34.6	0.2–380	0.11
Semipalmated Sandpiper	77	−0.084 ± 0.033	−8.08	−56.9	0.3–47,691	0.01
Least Sandpiper	71	−0.077 ± 0.028	−7.43	−53.8	0.3–153	0.007
White-rumped Sandpiper	57	−0.0003 ± 0.030	−0.03	−0.27	0.3–203	0.99
Dunlin	40	−0.005 ± 0.022	−0.54	−5.23	0.3–53	0.81
Short-billed Dowitcher	55	−0.068 ± 0.030	−6.52	−49.1	0.3–73	0.03

[a] Based on mean counts during peak adult migration periods. Sites weighted by precision of estimate only.
[b] Weighted mean slope on log scale.

TABLE 4

WEIGHTED POPULATION TRENDS CALCULATED USING ROUTE REGRESSION METHODS FOR SELECTED SHOREBIRD SPECIES DURING THE PERIOD 1974–1983

Species	No. sites	Range of mean counts	Percent annual change		
			A[a]	B[b]	C[c]
Black-bellied Plover	54	1–278	−8.49*	−8.29	−5.4*
Lesser Golden-Plover	18	0.2–1.4	+0.14	−0.69	
Semipalmated Plover	57	0.7–573	+2.77	−7.50	−9.5
Willet	33	0.3–66	−2.83	−4.52	+0.2
Whimbrel	26	0.3–24	−15.4	+1.15	−8.3***
Ruddy Turnstone	46	0.3–61	+4.74	−3.87	−8.5
Red Knot	31	0.3–53	−25.9	+4.74	−11.7
Sanderling	39	0.2–380	−4.37	−6.83	−13.7***
Semipalmated Sandpiper	57	0.3–63,963	−9.64	−10.6*	−6.7
Least Sandpiper	51	0.3–968	−14.7	−1.87	+2.9
White-rumped Sandpiper	32	0.3–28	−16.2	−3.65	
Dunlin	26	0.3–43	−12.2	−7.63	
Short-billed Dowitcher	45	0.3–525	−7.80	−7.92	−5.5**

* $0.1 > P > 0.05$; ** $P < 0.05$; *** $P < 0.01$.
[a] Slope precision × mean count weighting.
[b] Slope precision only weighting.
[c] Howe et al. 1989.

highly and significantly correlated. Differences resulted from the two weighting procedures emphasizing trends from different sets of sites.

Trends during the period 1974–1983.—Route regression analysis using slope precision × mean count weighting (Table 4) indicated that 10 of the 13 species had negative trends ranging from −2.83%/year for the Willet to −25.9%/year for the Red Knot. Calculated trends were generally larger (10 of 13 were greater than 3%/year) than those derived from the entire study period 1974–1991, reflecting the larger changes which appeared to be taking place in populations during the 1970s (see below). The strong overall negative trend across species was significant using a two-tail Wilcoxon signed rank test ($P < 0.01$). When trends were weighted by slope precision only, 11 of the 13 species showed declines (significant trend across species, Wilcoxon signed rank test, $P = 0.01$), although only that for the Semipalmated Sandpiper reached borderline statistical significance ($0.01 > P > 0.05$, see Methods) (Table 4).

Trend estimates derived by Howe et al. (1989) from ISS data for the period 1972–1984 are compared with those calculated from MSS data for the comparable period 1974–1983 in Table 4. A borderline significant negative trend was noted for Black-bellied Plovers in both studies. The significant negative trends found by Howe et al. for Whimbrel, Sander-

TABLE 5

TRENDS IN SHOREBIRD POPULATIONS AT 15 MSS SITES COVERED FOR EIGHT OR MORE YEARS DURING THE 17-YEAR PERIOD 1974–1990 USING THEIL'S NON-PARAMETRIC TEST BASED ON LOG-MEAN COUNT ANNUAL INDICES

Species	Score	*P*
Black-bellied Plover	−5	0.08
Lesser Golden-Plover	−37	0.24
Semipalmated Plover	+51	0.40
Willet	−20	0.65
Whimbrel	+72	0.11
Ruddy Turnstone	+9	0.90
Red Knot	−69	0.10
Sanderling	−22	0.68
Semipalmated Sandpiper	−146	0.02
Least Sandpiper	−115	0.05
Dunlin	−14	0.79
Short-billed Dowitcher	−88	0.08

ling, and Short-billed Dowitchers were also negative, although not significantly so, in the present study. Four of the trend estimates differed in sign between the two studies, although the differences did not reach statistical significance.

Trend estimates using Theil's test.—Two species, the Semipalmated Sandpiper and Least Sandpiper, showed significant declines during the period 1974–1990. Three other species showed declines which were of borderline significance, the Black-bellied Plover, Short-billed Dowitcher and Red Knot. The Whimbrel showed borderline increase (Table 5).

Changes in mean abundance: paired t*-test comparisons.*—Most species decreased in abundance during the study (Table 6), particularly between early and middle years, when 12 of the 13 species declined on average, a significant tendency across species (Wilcoxon signed rank test, $P < 0.01$). Three species showed significant or borderline significant declines, and the average mean decrease across all species was significantly different from zero.

Differences were less consistently negative between recent and middle counts. Eight of the 13 species showed declines (not a significant tendency across species, Wilcoxon signed rank test), only one of which was of borderline significance.

Recent counts were generally lower than those made in early years. Declines were noted in eight of the 13 species, an almost significant ($0.1 > P > 0.05$, Wilcoxon signed rank test) tendency across species. Four

TABLE 6

DIFFERENCES IN AVERAGE LOG-MEAN COUNTS OF SHOREBIRDS AT MSS SITES DURING "EARLY" (1974–1979), "MID" (1980–1985) AND "RECENT" (1986–1991) YEARS OF THE STUDY PERIOD USING PAIRED *T*-TEST COMPARISONS

	N	Difference in average log-mean counts					
		Mid–early	*P*	Recent–early	*P*	Recent–mid	*P*
Black-bellied Plover	223	−0.372	0.14	+0.226	0.51	+0.018	0.92
Lesser Golden Plover	221	−0.239	0.22	+0.096	0.44	+0.010	0.90
Semipalmated Plover	207	−0.160	0.63	−0.196	0.54	−0.085	0.78
Willet	159	+0.215	0.26	+0.128	0.38	−0.059	0.61
Whimbrel	177	−0.116	0.17	+0.004	0.98	−0.117	0.48
Ruddy Turnstone	198	−0.354	0.18	−0.026	0.92	+0.317	0.17
Red Knot	188	−0.013	0.94	−0.611	0.02	−0.281	0.10
Sanderling	207	−0.616	0.07	−0.494	0.13	−0.107	0.54
Semipalmated Sandpiper	188	−0.347	0.16	−1.246	0.00	−0.329	0.25
Least Sandpiper	197	−0.410	0.29	−1.037	0.005	−0.214	0.35
White-rumped Sandpiper	195	−0.722	0.02	+0.184	0.49	+0.255	0.26
Dunlin	124	−0.150	0.60	−0.064	0.87	+0.135	0.58
Short-billed Dowitcher	159	−0.655	0.03	−0.757	0.03**	−0.097	0.62
Mean difference		−0.303		−0.292		−0.043	
SD		0.267		0.489		0.191	
N		13		13		13	
t[a]		−4.096**		−2.153*		−0.804	ns

[a] Comparison of mean difference with 0, ns = not significant, * = $0.1 > P > 0.05$; ** = $P < 0.05$.

species declined significantly, and the average decrease for all species approached statistical significance ($t = -2.153$, $P = 0.052$).

These results suggest that numbers of shorebirds declined during the study period, with the greatest decreases occurring during the early years of the study.

Population trends during early, middle and recent years of the study period.—Route regression analysis showed that population trends differed considerably in both rate and direction during different phases of the study period (Table 7). Results using slope precision × mean count weighting showed that nine of the 13 species declined during the early (1974–1979) period. Two species showed significant negative trends, two showed borderline significant declines, and one showed a borderline increase. In contrast, during the middle period (1980–1985), 11 of the 13 species analyzed showed positive trends, five of which were statistically significant. The overall positive trend across species was statistically significant (Wilcoxon signed rank test $0.02 < P < 0.05$). During more recent years (1986–1991), declines and increases were more evenly matched, with one sig-

TABLE 7

SHOREBIRD POPULATION TRENDS (ANNUAL PERCENT CHANGE) CALCULATED USING ROUTE REGRESSION ANALYSIS FOR EARLY (1974–1979), MID (1980–1985) AND RECENT (1986–1991) SUBSETS OF YEARS

	1974–1979			1980–1985			1986–1991		
		Trend			Trend			Trend	
Species	N	A[a]	B[b]	N	A[a]	B[b]	N	A[a]	B[b]
Black-bellied Plover	42	−6.77*	−15.9*	25	+2.15	+19.0	31	−2.41	+1.44
Lesser Golden-Plover	12	+46.6	−1.36	8	−10.8	−7.46	12	−32.6	−16.9
Semipalmated Plover	46	−5.40	−16.8*	24	+29.3**	+10.5	35	+16.8***	+1.85
Willet	28	−3.44	−10.1	12	+5.31	+22.8	12	+2.44	−3.71
Whimbrel	21	+20.7*	+12.0	12	+30.9	−1.12	14	−3.43	−16.4
Ruddy Turnstone	38	+8.46	−4.02	20	+33.4***	+30.4**	27	−0.49	+9.46
Red Knot	24	+51.4	+8.43	13	+3.37	+4.72	14	−21.3***	−0.65
Sanderling	31	−25.4***	−16.2*	18	+24.4***	+17.3	17	+0.15	−3.68
Semipalmated Sandpiper	44	−14.0	−23.6*	23	+8.80**	+6.85	31	+33.7	−14.2
Least Sandpiper	40	−23.0	−12.0	21	+9.68	+13.1	30	+3.06	−6.92
White-rumped Sandpiper	27	−39.1*	−4.21	19	−21.5	+14.8	26	+8.87	−3.21
Dunlin	24	−13.3	−7.89	9	+39.5	−3.61	15	−15.0	−7.07
Short-billed Dowitcher	39	−16.2	−4.62	17	+54.8**	−1.02	17	−5.54	+22.4

* $0.1 > P > 0.05$; ** $P < 0.05$; *** $P < 0.01$.

[a] Weighted by slope precision estimate × mean count.

[b] Weighted by slope precision estimate only.

nificant trend in each direction. There was no overall statistically significant trend across species.

Analysis using slope-precision-only weighting indicated that 11 of the 13 species declined during the early period, a significant trend across species (Wilcoxon signed rank test, $P < 0.05$). Four of the declines were of borderline statistical significance. In contrast again, nine of the 13 species increased during the middle period, also a significant tendency across species (Wilcoxon signed rank test, $P = 0.02$). One positive trend was statistically significant. Although nine of the 13 species registered negative trends during recent years, none of the trends or the tendency across species was statistically significant.

Statistical power of the surveys.—Power analysis showed that a plus or minus 2% annual population change would be detected at 80% power for all species except Lesser Golden-Plover and Whimbrel for coverage of 40–50 sites for the number of years on which the trend analyses were based (18). A 5% population change would be detected at 80% power for all species for this degree of coverage. Coverage required to achieve 80% power varied between species and was typically 12–18 years for 40 sites to detect a 2% change and 9–15 years for 20 sites to detect a 5% change. Slightly longer coverage (approx. one year) was often required to detect decreases compared to increases. The present MSS coverage should thus be adequate to detect the levels of changes found in the trend analysis.

DISCUSSION

Data analysis.—Route regression methods use log-transformations of data and assume that trends are constant both during the study period and at different sites and that changes are representative of the population being sampled. Assumptions that ISS data were log-normally distributed were tested by Howe et al. (1989) and found to be generally acceptable. While they were not formally tested in the present study, analysis (unpubl. data) has shown that the MSS data mostly conform to a negative binomial distribution for which log-transformations would be reasonable. Log-transformations are also advantageous in stabilizing variance estimates and producing linear regressions for constant annual population trends.

Assumptions that trends are constant across sites or through time are unlikely to be met. There is no a priori reason to assume that population trends will be constant over time. Indeed, route regression analysis of data from subsets of years of the present study indicated that trends of very different magnitude and direction were taking place. Analysis of data from individual sites also showed that trends were not constant either in time or direction (unpubl. data). Where short-term variations are part of

an underlying long-term trend, route regression methods will still be valid in assessing the direction and magnitude of the long-term trends.

Use of several statistical techniques and weighting methods offers a more complete perspective on population trends for conservation purposes than use of a single method, since different aspects of the data are emphasized. With route regression analysis, weighting by slope precision is always desirable, since sites with imprecise slope estimates, which could otherwise exert a considerable effect on the overall trend calculation (larger values of slopes were always associated with imprecise estimates), are effectively downweighted or removed. Slope-precision-only weighting, however, also results in many types of sites, including ones with high and low numbers of birds, contributing effectively to the trend estimate. Results from this method thus reflect trends occurring across a broad range of sites. With mean count × slope precision weighting, on the other hand, results principally reflect trends occurring at sites with large numbers of birds, especially where such sites have both high numbers of birds and a precise slope estimate.

Results from both types of analysis provide complementary information for conservation purposes. Detection of changes occurring across a broad range of sites is of basic importance, because declines may first be seen at sites with peripheral habitat before they become apparent at sites with optimal habitat. On the other hand, changes occurring at sites that support particularly high numbers of birds, and which might be masked in the former analysis, may reflect habitat changes or other problems which could affect a significant proportion of the population.

Theil's analysis and paired *t*-tests, in contrast to regression techniques, do not make any assumptions about the direction or rate of change of populations. Theil's slope analysis involves a non-parametric ranking procedure and may be less sensitive to outliers in the data resulting from unrepresentative counts being obtained in a given year at a particular site. Neither Theil's or paired *t*-test analyses use weighting procedures and may thus reflect trends occurring across a broad range of sites, although *t*-test comparisons could be affected by an unrepresentative high count affecting a site mean.

These considerations suggest that a combination of analytical methods will be most appropriate for examining population trends based on count data obtained from the volunteer survey network operation.

Population trends.—All three methods used for analyzing Maritimes Shorebird Survey data indicated declines in shorebird populations in eastern Canada during the period 1974–1991. The species for which declines were most consistently recorded were the Least Sandpiper, Semipalmated Sandpiper, and Short-billed Dowitcher. Decreases for Red Knot and

Black-bellied Plover approached statistical significance in some analyses. The preponderance of declines across the 13 species analyzed was often significant. Declines occurred in most species during the latter part of the 1970s, whereas most species increased during the first half of the 1980s. Changes since 1985 do not appear to have been as marked in either direction.

Causes of declines in shorebird populations are potentially complex and may occur at many points during the annual cycle of the birds. In eastern North America, possible causes of declines include loss of critically important habitat which may result from man-induced or natural causes, pollution, weather, and increased disturbance from human activities or predators. In Europe, Goss-Custard and Moser (1988) reported that decreases in numbers of Dunlin wintering in the U.K. was most pronounced on estuaries where the spread of cord grass (*Spartina anglica*), which is known to hold reduced densities of prey (Millard and Evans 1984), had been greatest. Increased levels of disturbance to roosting Bar-tailed Godwits and Red Knots were thought to be the principal cause of major declines in numbers of those species roosting on the Dee Estuary (Mitchell et al. 1988). Disturbance was also thought to be a major factor affecting the quality of roost sites and hence numbers and distribution of shorebirds on the Firth of Forth (Furness 1973). Shorebirds on migration are particularly vulnerable to such changes owing to their need to store fat reserves for long onward flights, especially those species making very long distance movements (Evans 1991, Evans et al. 1991). Some species may need to accumulate sufficient energy reserves not only for migration but also for subsequent survival and reproduction on High Arctic breeding grounds (Morrison and Davidson 1990).

Widespread losses have occurred in wetland habitats in eastern North America during the present century (Senner and Howe 1984, Bildstein et al. 1991). Such losses would not necessarily affect different species to the same extent, since the main migration areas for different species are found in different areas (Harrington and Morrison 1979, Morrison 1984, Harrington et al. 1989, Morrison and Harrington 1992). There are, in fact, many differences in the migration patterns and characteristics of the species analyzed in the present study. Their breeding ranges occupy wide regions of the Arctic, from middle and high latitudes to low Arctic and boreal areas, stretching from the eastern to the central Arctic. Their wintering grounds lie from the southern tip of South America through its northern coast to the southern United States. They feature long-, middle- and relatively short-distance migrants. They are of a wide variety of sizes and morphologies. All occur in large concentrations during migration and on the wintering areas, making them vulnerable to environmental change.

Apparent decreases (or increases) in shorebird populations in eastern Canada might result from shifts in distribution of shorebirds either within the Atlantic Provinces of Canada themselves or on a broader scale over the eastern seaboard of North America. Possible shifts in distribution of Semipalmated Sandpipers within the upper Bay of Fundy are suggested by the contrast between declining counts at Mary's Point, N.B. (unpubl. data) and apparent increases at other nearby sites in recent years (P. Hicklin, pers. comm.). Declining counts at Mary's Point will have contributed strongly to the negative trend (not significant) found during route regression analysis of MSS data using mean × slope precision weighting, owing to the large numbers of birds which occur there. However, the analysis using slope-precision-only weighting, which reflects trends occurring at a much broader range of sites, showed an even more negative (and statistically significant) trend for the species, suggesting decreases had occurred over a wide area.

Other considerations indicate that the MSS protocol should detect trends that are representative of those occurring over a wider area and that similar populations of shorebirds are being sampled from year to year. The wide distribution of sites across the Atlantic Provinces of Canada in itself provides a broad geographical basis for analyzing population trends. Trends at MSS and ISS sites (Howe et al. 1989) were similar during the 1970s, indicating a consistent pattern over much of the eastern seaboard of North America. Sites were not selected on a random basis but were chosen by participants for a variety of reasons, including use by large numbers of shorebirds and convenience of coverage. However, many species of shorebirds are highly consistent in their use of stopover areas on migration (Morrison 1984, Smith and Houghton 1984), indicating that similar populations are being sampled at a given site from year to year. The possibility that birds might overfly the Maritime Provinces and make a direct flight to wintering areas farther south (e.g., in South America) in years in which they were in unusually good condition seems unlikely on the basis of their potential flight range capabilities from sites in the interior or farther north (e.g., James Bay, Morrison 1984). They might, however, pass through farther south on the eastern seaboard of the United States, although there is currently no evidence that this occurs. Distribution patterns appear consistent from year to year, and few major concentrations of shorebirds are found in other parts of eastern Canada (Morrison et al. 1991).

Weather on the breeding grounds might affect shorebird populations on a broad scale. Boyd (1992) noted that mean June temperatures at locations in the eastern Canadian High Arctic were particularly low during the 1970s and that numbers of Red Knots from these breeding areas

wintering in the U.K. tended to fall after cool Junes and rise after warm ones. In 1974, severe weather in mid-June on Ellesmere Island and in other parts of the High Arctic zone in Greenland resulted in many knots and turnstones dying of starvation (Morrison 1975). Similarly severe weather occurred in other parts of the Arctic during the latter part of the 1970s (unpubl. data) and may have affected shorebird populations passing through the eastern seaboard of North America. Increases in populations during the early 1980s occurred during a period of less severe weather across the Arctic (unpubl. data).

Shorebirds face threats from a variety of sources throughout their migration ranges (Morrison 1991). While weather on the Arctic breeding grounds may currently appear to be one of the most likely factors to have influenced shorebird populations migrating through the eastern seaboard of North America over the past 15–20 years, the possible impact of other potential threats must not be ignored. Ongoing shorebird surveys and monitoring schemes have an important role to play not only in assessing the health of shorebird populations but also in determining the processes influencing population levels and in designing conservational initiatives based on an understanding of the biology of the species concerned.

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Wilson Bull., 106(3), 1994, pp. 448–455

DEVELOPMENT AND MAINTENANCE OF NESTLING SIZE HIERARCHIES IN THE EUROPEAN STARLING

THOMAS OHLSSON AND HENRIK G. SMITH

ABSTRACT.—In this paper we show that nestling mass hierarchies in the European Starling (*Sturnus vulgaris*) are due to asynchronous hatching. The parents may, by starting to incubate the day the penultimate egg is laid, or earlier, affect the degree of hatching asynchrony and thereby the nestling weight hierarchy. Intra-clutch variation in egg size had no effect on nestling weight hierarchies, explaining only 0.4% of the variation in nestling mass at two days of age. Nestlings kept their relative size to siblings throughout a substantial part of the nestling period. Furthermore, the degree of variation in mass at two days of age affected the variation in mass at least until nine days. This relationship was stronger in larger broods. *Received 13 Sept. 1993, accepted 30 Jan. 1994.*

For most or all bird species, the conditions for raising young are unpredictable. If the nestlings within a brood compete with each other for food, selective brood reduction might be beneficial for the parents when there is not enough food for all nestlings to survive (Lack 1947). Hence, in unpredictable environments, it might be beneficial for parents to create a size hierarchy among nestlings to facilitate early brood reduction when food is scarce. There are at least two ways for parents to create nestling size hierarchies. First, in most bird species incubation starts before the last egg is laid, with the result that one or several nestlings hatch after their siblings (Clark and Wilson 1985). Second, the variation in egg size with laying sequence might contribute to nestling size hierarchies if, for example, late laid eggs are smaller (Rydén 1978, Slagsvold et al. 1984). However, it is not well known how hatching asynchrony and egg size variation contribute to nestling size hierarchies (Magrath 1990). For example, nestling size hierarchies may develop soon after hatching, even when hatching is synchronous (Clark and Wilson 1981), and egg size variation might be too small to contribute to variation in nestling mass (Magrath 1990). Furthermore, if the feeding rates of individual nestlings are under parental control, size hierarchies may not have any important effect on the growth rate and mortality risk of nestlings.

The aim of this paper is to show how nestling size hierarchies in the European Starling (*Sturnus vulgaris*) are affected by natural variation in hatching asynchrony and egg size and to assess if early size hierarchies are maintained during the early nestling period.

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METHODS

We studied starlings from March to June 1992, in the Revinge area (55°42′N, 13°28′E), 20 km ESE of Lund, in southern Sweden. The area is characterized by open pastures grazed by cattle, interrupted by shrub and small forests. Starlings bred in 11 colonies containing 12–15 nestboxes of similar size. During the egg laying period, nestboxes were visited once daily between 10:00 and 13:00 h. Eggs were marked individually with an indelible marker the day of laying and weighed to the nearest 0.05 g using a 10-g Pesola spring balance mounted in a glass-tube (as a wind-shield). If two new eggs were discovered in a nest on the same day, one of them was considered to have been laid by a parasite female (Feare 1984). In this study, the parasite's egg always was easy to recognize, since it differed from the other eggs in size, color, and/or shape (see Stouffer et al. 1987, Evans 1988). Eggs of parasites were transferred to other nests not included in this study. Eggs occasionally were thrown out during laying, presumably by a parasitic female (Lombardo et al. 1989). In five cases, one egg was missing or destroyed and replaced with another unincubated egg of similar mass. The majority of the nests included in this study were subject to an experimental study on the effect of egg size on fitness (Smith et al., in press). The experiment consisted of switching similar-sized clutches completed on the same day. Switching occurred the day after clutch completion. Since the purpose of this study was to evaluate how variation in egg size and hatching spread affected nestling size hierarchies, rather than the effect of parental attributes, we pooled data from the experimental and control broods. This study included a total of 31 clutches from the experiment, six sham-manipulated clutches (eggs temporarily removed) and four control broods.

Nests were visited daily between 07:00 and 17:00 h. Newly hatched chicks were weighed and marked with a segment of a drinking straw around their tarsi (Harper and Neill 1990). The age of hatchlings was estimated using a method described by Stouffer and Power (1990). Hatchlings were estimated to be, on average, 1.5 h old if they had red skin and wet down, and on average, 4.5 h old if they had red skin and dry down, and older if their skin had turned yellow. Nestlings were weighed when they were 1, 2, 3, 4, 5, 6, 7, 9, 11, and 14 days old (day 0 being the day of hatching). Nestboxes were visited later in order to determine if any nestlings failed to fledge.

Statistics were performed with SYSTAT (Wilkinson 1990). We tested for interactions in all multivariate analyses but excluded them unless significant. For cases where we had ordered expectations, isotonic regression was used (Gaines and Rice 1990).

RESULTS

The degree of size hierarchy among nestlings was affected by the nestlings' spread in hatching time. For this analysis we only included nestlings whose hatching time was well known (i.e., encountered when still red) and only broods where this was known for at least four nestlings. This left 15 nests in which, on average, 4.4 out of 5.5 nestlings had known hatching times. In only one case was the hatching time of the last-hatched young not known. Since all nestlings were not hatched until day 2, we used mass day 2 to calculate the dependent variable. Following Harper et al. (1993), we used the coefficient of variation as the measure of the hierarchy. Variation in mass at day 2 was positively related to the variation in hatching time (Fig. 1). When estimating the effect of the variation in egg mass on nestling size hierarchies, we used only clutches where we

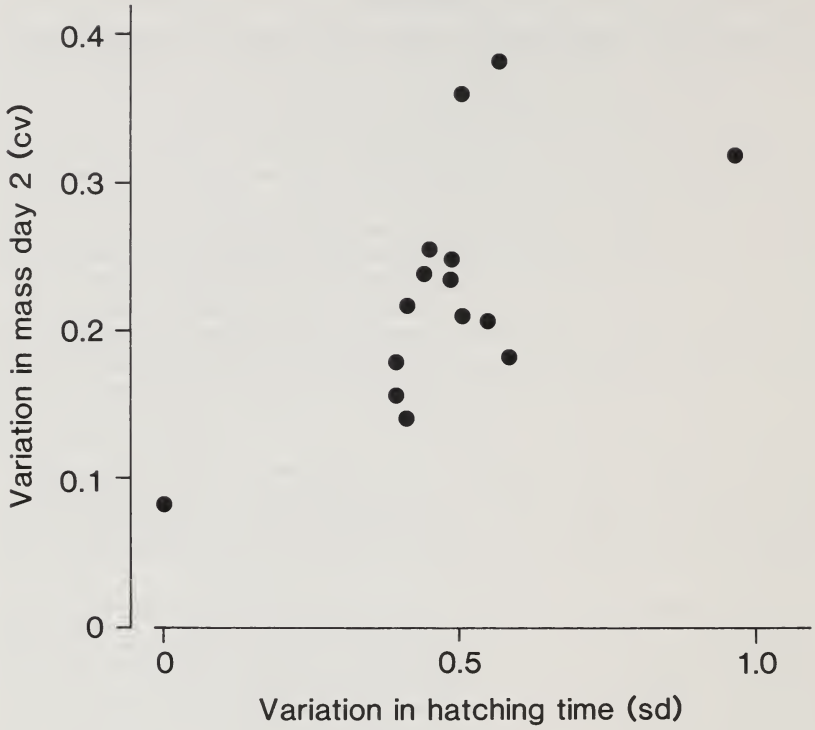

FIG. 1. The relationship between the coefficients of variation for nestling mass at two days post-hatching and the standard deviation of hatching spread. $r_s = 0.62$, N = 15, $P < 0.02$.

knew the masses of all hatched eggs that were also not subject to partial mortality before two days of age. The coefficient of variation in mass of nestlings two days after hatching was not affected by the coefficient of variation in egg mass ($F_{1,45} = 0.18$, $P = 0.68$). In fact, only 0.4% of the variation was explained by egg mass variation. The results were the same also when different brood sizes were analysed separately ($P > 0.1$ in all cases).

When estimating the persistence of size hierarchies, we only included broods where at least three nestlings still could be identified (from day 11 some nestlings lost their bands). We estimated the persistence of size hierarchies among nestlings in two ways. First, for each brood we related the mass of nestlings at varying ages to their mass when two days old. This analysis demonstrated that the relative sizes of nestlings were kept

TABLE 1

THE RELATIONSHIP BETWEEN NESTLING MASS AT VARIOUS AGES TO THEIR MASS WHEN TWO DAYS OLD TESTED WITHIN BROODS USING PEARSON CORRELATION

Age (days)	+[a]	−[a]	*P*
3	41	0	<0.0005
4	41	0	<0.0005
5	37	1	<0.0005
6	38	0	<0.0005
7	39	0	<0.0005
9	33	0	<0.0005
11	28	2	<0.0005
14	11	3	0.11

[a] The number of broods with positive and negative relationships at various ages.
[b] Significance tested with sign test.

until at least 11 days after hatching (Table 1). The lack of significance at 14 days of age is probably due to the decline in sample size caused by nestlings losing their bands. Interestingly, there was a tendency for the slope of the relationship between nestling mass at 11 days of age and that when two days old to be higher when brood size was higher (isotonic regression on slopes for broods of size 4, 5, and 6, $E_3^2 = 0.13$, $P = 0.063$; see also Fig. 2), indicating that hierarchies may be maintained to a higher degree when broods are larger. Secondly, we related the amount of variation in mass at various ages to the amount of variation at two days of age. These analyses showed that the magnitude of the mass hierarchy

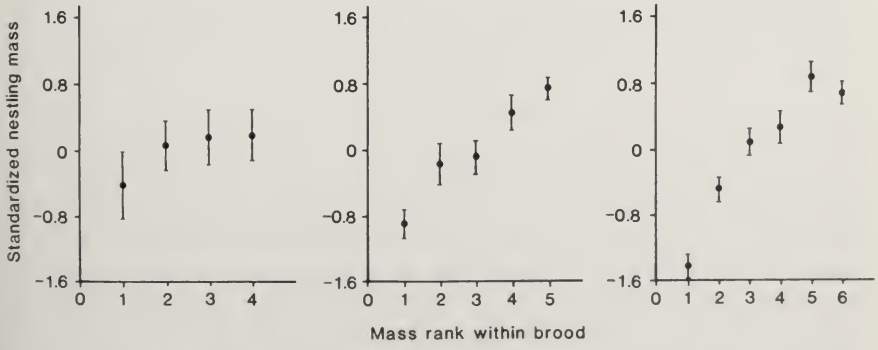

FIG. 2. The relationship between mass of nestling starlings when 11 days old and the relative rank of mass within broods (1 being the smallest) when two days old for broods of 4, 5, and 6 nestlings. Nestling mass was standardized to a mean of zero and a variance of one within broods.

TABLE 2

THE RELATIONSHIP BETWEEN THE COEFFICIENT OF VARIATION OF NESTLING MASS AT VARIOUS AGES TO THE COEFFICIENT OF VARIATION AT TWO DAYS OF AGE FOR STARLING BROODS

Age (days)	N	r^a	*P*
3	41	15.160	0.001
4	42	8.822	0.001
5	40	5.211	0.001
6	40	5.684	0.001
7	41	5.928	0.001
9	34	3.439	0.002
11	32	1.282	0.210
14	17	1.184	0.255

[a] Tested with linear regression.

within broods was affected by the magnitude two days after hatching at least up to day 9 (Table 2; Fig. 3).

DISCUSSION

Adaptive brood reduction in variable environments is thought to be facilitated by nestling size hierarchies (Lack 1947). These nestling size hierarchies are in turn thought to be affected by both hatching spread (Magrath 1990) and egg size variation (Slagsvold et al. 1984). Accordingly, egg size variation and variation in hatching spread have been interpreted as adaptive (e.g., Rydén 1978, Slagsvold et al. 1984, Hussell 1985, Slagsvold 1986).

According to the brood-reduction hypothesis, the last-laid egg should be smaller than the other eggs in the clutch (Slagsvold et al. 1984) to contribute to the development of nestling size hierarchies (Slagsvold et al. 1984). However, our study demonstrates that egg size variation has at the most a very weak effect on nestling size hierarchies. Other studies have also found that egg mass accounted for only a small proportion of the variation in nestling mass (Bryant 1978, Bancroft 1984, Stokeland and Amundsen 1988). Mead and Morton (1985) demonstrated for the White-crowned Sparrow (*Zonotrichia leucophrys*) that although the last-hatched chicks came from larger eggs, they turned out to be smaller than their siblings due to asynchronous hatching. It seems likely that variation in egg size within clutches of passerines is of minor importance for establishing weight hierarchies. Hence, rather than being interpreted adaptively, variation in egg mass within clutches might arise as a consequence of nutritional constraints on the female during egg-laying (Järvinen and Ylimaunu 1986, Slagsvold and Lifjeld 1989, Nilsson and Svensson 1993).

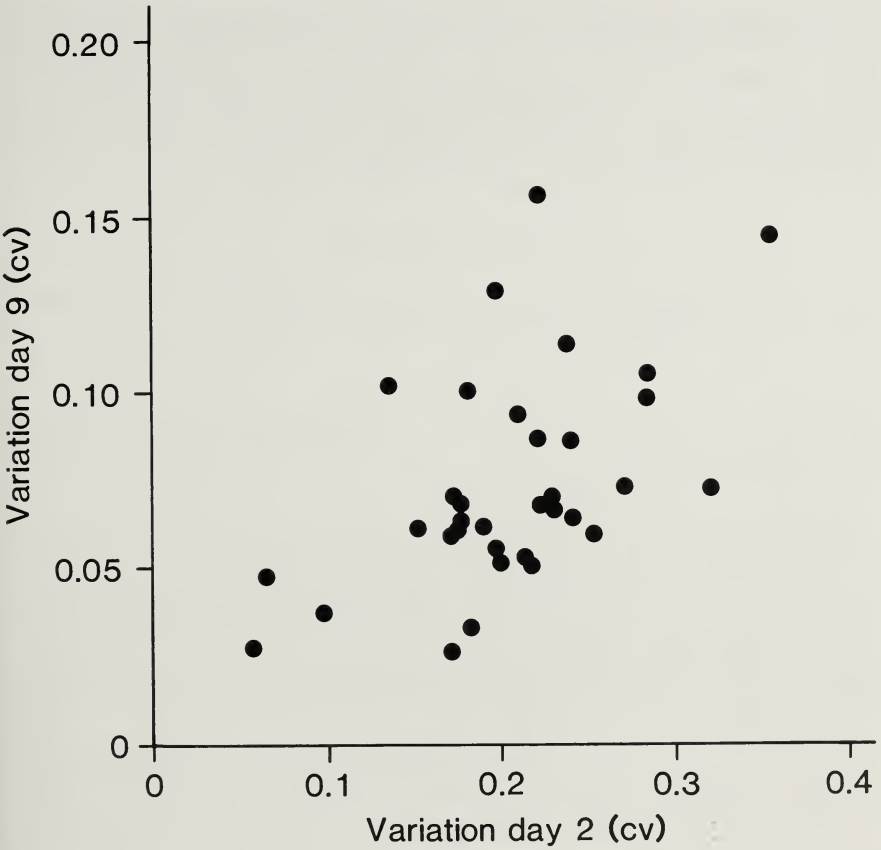

FIG. 3. The relationship between the coefficient of variation of mass within starling broods when nine days old to that of nestlings when two days old. For statistics see Table 2.

We found that the nestling size hierarchy among starlings reflected the hatching order of the chicks. Furthermore, the size of the hierarchy reflected the degree of hatching spread. Other studies also have shown that the most important reason for the development of weight hierarchies among nestlings is the difference in hatching time within the brood (Bryant 1978, Magrath 1992). This has also been experimentally confirmed for European Starlings by manipulating the incubation time of individual eggs (Stouffer and Power 1991). Hence, parents may determine the degree of mass variation within broods, and thereby the likelihood for brood reduction (Bryant 1978), by regulating at what stage they begin to incubate (Magrath 1992).

The initial nestling size hierarchy persisted during most of the nestling phase, but its importance decreased with the age of nestlings. Interestingly, the early size hierarchy tended to be more persistent in large broods. This could mean that sibling competition is more lax in smaller broods, enabling the smaller chicks to grow faster. Furthermore, in smaller broods nestlings might reach their asymptotic mass earlier.

ACKNOWLEDGMENTS

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1994 NABS RESEARCH AWARDS

The North American Bluebird Society is pleased to announce the results of its tenth annual research grant's program. The following individuals are recipients of the 1994 research awards:

BLUEBIRD GRANTS

Rachel F. Holt, University of British Columbia. Title: Population Regulation of Mountain Bluebirds Nesting in Clear Cuts: The Changing Roles of Nest Site Limitation, Predation and Vegetation Succession.

Daniela S. Monk, Indiana University. Title: Differential Allocation of Parental Care in Mountain Bluebirds.

Gary L. Slater, University of Florida. Title: Nest Site Limitation and Competition: Effects on Eastern Bluebird and Brown-headed Nuthatches in Southern Florida Threatened Pineland Ecosystem.

STUDENT GRANTS

Jeffrey F. Kelly, Colorado State University. Title: The Effect of Food Availability on Behavior and Reproduction of Belted Kingfishers.

Sheldon J. Cooper, Utah State University. Title: Physiological, Physical, and Behavioral Adaptations to Cold in the Mountain Chickadee and the Plain Titmouse.

Colleen A. Barber, Queen's University. Title: Determinants of Extra-pair Paternity in Tree Swallows.

GENERAL GRANTS

Drs. E. Dale Kennedy and Douglas W. White, Kansas State University. Title: Breeding Biology of Bewick's Wren: Conservation Implications.

Dr. Charles R. Blem, Virginia Commonwealth University. Title: Clutch Size, Rate of Growth, and Reproductive Success of Prothonotary Warblers.

Wilson Bull., 106(3), 1994, pp. 456–465

A CAMERA STUDY OF TEMPORAL PATTERNS OF NEST PREDATION IN DIFFERENT HABITATS

JAROSLAV PICMAN[1] AND LYNN M. SCHRIML[1]

ABSTRACT.—We examined composition of predator communities, relative importance of individual nest predators, and temporal patterns of nest predation in marsh, old field, scrubland, and forest habitats. To record predation, we photographed animals manipulating Japanese Quail (*Coturnix coturnix*) eggs in artificial dry grass nests. A total of 848 photos of nest visitors was obtained in all habitats by means of automatic cameras. The number of different species of egg predators/destructors was low in the marsh (4 species), intermediate in the old field (6 species), and higher in the scrubland and forest (9 species). However, in each of the four habitats there were only one or two major predators. The temporal patterns of predation differed between habitats and were mostly determined by the relative importance of mammalian (mostly nocturnal) and avian (exclusively diurnal) predators. *Received 12 April 1993, accepted 7 Oct. 1993.*

Although predation may be the major cause of nesting mortality of most species (e.g., Lack 1968, Ricklefs 1969), its role as a selective force shaping avian reproductive strategies has not been thoroughly examined. To understand predation as a selective force, we need data on temporal patterns of activities of different predators. More specifically, we need to establish the extent and relative importance of diurnal and nocturnal predation because predators operating at different times of day should present different selective pressures. The purposes of our study, therefore, were to (1) identify predators that attack passerine clutches in four different habitats (marsh, old field, scrubland, forest), (2) determine their relative importance, and (3) examine the temporal pattern of nest predation in these habitats.

METHODS

Between May and July 1986, we established automatic camera stations in four habitats (marsh, old field, scrubland, and forest) in the Mer Bleue Bog Conservation Area near Ottawa, Ontario, Canada (coordinates 45°23′N, 75°32′W). The marsh is extensive (about 30 ha; maximum water depth in the marsh center is about 120 cm) and has a relatively homogeneous cattail (*Typha* sp.) cover up to 220 cm high. The old field is a meadow habitat adjacent to the marsh, with grasses and various herbs dominating the plant community. The vegetation cover is low (a maximum of about 50 cm when the study was conducted). The scrubland was also adjacent to the marsh. Dominant shrubs in this habitat were meadow sweet (*Spirea* spp.) and willow (*Salix* spp.); of occasional trees, birch (*Betula* spp.) was most common. Shrubs and trees were interspersed in this habitat with small patches of grass. The forest was about 3 km from the other habitats and was dominated by mature, approximately 50-year-old deciduous and coniferous trees such as maple (*Acer* spp.), American

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beech (*Fagus grandifolia*), oak (*Quercus* spp.), birch (*Betula* spp.), spruce (*Picea* spp.), and Pine (*Pinus* spp.).

In each of the four habitats we established three 80 m × 80 m quadrats (neighboring quadrats were 20 m apart). In these quadrats, we offered predators experimental nests with Japanese Quail (*Coturnix coturnix*) eggs (depending on experiment, between 9 and 40 nests/quadrat and 1 egg/nest). We constructed experimental nests from dry grass (in size and shape similar to Red-winged Blackbird [*Agelaius phoeniceus*] nests). We distributed these nests with eggs according to random, clumped, and uniform spacing patterns (40 nests/quadrat) and in different densities (40, 25, and 9 nests/quadrat) throughout the experimental quadrats (results of these experiments will be reported elsewhere). In addition, in each habitat, 20 m from these quadrats, we placed a transect of 10 camera setups 10 m apart. Each camera setup consisted of a camera, a dry grass nest with one quail egg, and a mechanism that triggered the camera when a predator manipulated an egg (Picman 1987). Some camera setups were also equipped with a clock, placed approximately 30 cm from the nest, which allowed recording time when pictures of the predation events were taken (Picman 1987).

In each habitat, we had one transect with 10 camera setups (i.e., a total of 40 camera setups were operated simultaneously). Every two weeks we moved the camera transects to a new location (at least 100 m away from the original location) to reduce effects of habituation by predators to the nest location and to sample predation over a larger area. We operated the camera transects from the beginning of May until the end of July, 1986 (92 days, 3680 camera days, 920 in each habitat). We visited all setups once a day (usually between 09:00 and 12:00), replaced depredated eggs with new eggs, and re-set cameras. We kept notes on the appearance of depredated eggs and on the time of predation events.

In the marsh, scrubland, and forest, we placed all nests 80–100 cm above ground (we attached nests to wooden stakes; see Picman 1987). We placed the camera setups in concealed locations (i.e., in dense vegetation) to simulate natural nest locations. In the old field, we placed nests on the ground to simulate passerines breeding in the grassland. For this reason, we had to shorten wooden stakes supporting the cameras so that, in the old field, the cameras would be approximately 20 cm above ground.

RESULTS

We obtained a total of 878 photos of different nest visits by eight mammalian (368 photos) and 17 bird (510 photos) species. To establish the status (i.e., predator vs accidental visitor) of individual species, we used information on the outcome of nest visits by individual species. In most cases, the mammalian visitors destroyed the quail eggs (Table 1), and we thus consider them as potential egg predators. Our results suggest that the striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), and red squirrel (*Tamiasciurus hudsonicus*) are the most important nest predators. These species were responsible for 96% of all mammalian predation events in our study area. The remaining mammals recorded by our cameras (short-tailed weasel [*Mustela erminea*], flying squirrel [*Glaucomys volans*], deermouse [*Peromyscus maniculatus*], chipmunk [*Eutamias* sp.], and woodchuck [*Marmota monax*]) were infrequent visitors at nests and had a small impact on experimental clutches.

TABLE 1

TOTAL NUMBER OF PHOTOGRAPHS OF PREDATORS AT EXPERIMENTAL NESTS IN DIFFERENT HABITATS

Predator	No. of photographed predation events in				Total	Percent of nest visits when eggs depredated
	Marsh	Meadow	Scrubland	Forest		
Raccoon	138 (46)[a]	2 (2)	13 (6)	62 (25)	215 (79)	97
Red squirrel	—	—	31 (8)	8 (8)	39 (16)	6
Short-tailed weasel	1 (1)	—	3 (3)	—	4 (4)	—
Flying squirrel	—	—	—	1 (1)	1 (1)	—
Deermouse	—	—	—	2 (2)	2 (2)	—
Striped skunk	—	101 (36)	—	—	101 (36)	100
Chipmunk	—	—	2 (2)	—	2 (2)	—
Woodchuck	—	4 (1)	—	—	4 (1)	—
Blue Jay	1 (1)	1 (0)	179 (82)	220 (202)	401 (285)	94
Broad-winged Hawk	—	—	—	14 (14)	14 (14)	91
Northern Harrier	2 (0)	1 (0)	—	—	3 (0)	—
Cooper's Hawk	—	—	—	1 (0)	1 (0)	—
Downy Woodpecker	—	—	—	1 (1)	1 (1)	—
Gray Catbird	—	—	6 (1)	—	6 (1)	—
American Crow	—	—	10 (5)	—	10 (5)	100
House Wren	—	—	2 (1)	—	2 (1)	—
Eastern Meadowlark	—	28 (6)	—	—	28 (6)	100
Red-winged Blackbird	29 (22)	—	—	—	29 (22)	21
Black-capped Chickadee	—	—	2 (2)	1 (1)	3 (3)	—
American Robin	—	—	—	1 (1)	1 (1)	—
Swamp Sparrow	1 (1)	—	—	—	1 (1)	—
American Goldfinch	—	—	7 (2)	—	7 (2)	—
Cedar Waxwing	—	—	1 (0)	—	1 (0)	—
Yellow Warbler	1 (1)	—	—	—	1 (1)	—
Thrush (sp. ?)	—	—	—	1 (1)	1 (1)	—
Total	173 (72)	137 (45)	256 (112)	312 (256)	878 (485)	
Total number of species	7	6	11	11	25	

[a] Number of events where time was recorded is given in parentheses. We assumed that broken or missing eggs were depredated. Percent of nest visits when eggs were depredated (i.e., were found broken or missing) was calculated for all photographed predation events for species of animals with at least 10 nest visits. Sample size: 920 nest days in each habitat.

TABLE 2

NUMBER OF PREDATORS IN THE FOUR HABITATS AS DETERMINED FROM PHOTOS OF PREDATION EVENTS

Habitat	Avian predators	Mammalian predators	All predators	Major predators[a]	Total
Marsh	2	2	4	1	142
Old field	3	3	6	2	137
Scrubland	5	4	9	2	248
Forest	5	4	9	2	310

[a] The major predators were defined as those that caused at least 10% of all cases of predation in a given habitat. Events that involved species not known to depredate on eggs or destroy eggs for other reasons were excluded from the total number of predation events in a given habitat. 920 nest days in each habitat.

Avian visitors included predatory birds such as (in the decreasing order of number of visits) Blue Jay (*Cyanocitta cristata*), Broad-winged Hawk (*Buteo platypterus*), American Crow (*Corvus brachyrhynchos*), Northern Harrier (*Circus cyaneus*), and Cooper's Hawk (*Accipiter cooperii*), all of which regularly destroyed the experimental eggs (Table 1). In addition to these predators, our cameras recorded visits of several species that are known to attack and destroy eggs of other passerines for reasons other than predation. These included the Gray Catbird (*Dumetella carolinensis*), House Wren (*Troglodytes aedon*), and Eastern Meadowlark (*Sturnella magna*); see Belles-Isles and Picman (1986a, b) and Picman (1992). Although the Black-capped Chickadee (*Parus atricapillus*) has been reported to attack eggs (Belles-Isles and Picman 1988), more recent data indicate that egg attacks are a relatively rare phenomenon in this species (J. Picman and S. Pribil, unpubl. data). We believe that eight bird visitors recorded by our cameras (Downy Woodpecker [*Picoides pubescens*], Swamp Sparrow [*Melospiza georgiana*], American Robin [*Turdus migratorius*], Red-winged Blackbird [*Agelaius phoeniceus*], American Goldfinch [*Carduelis tristis*], Cedar Waxwing [*Bombycilla cedrorum*], Yellow Warbler [*Dendroica petechia*], and an unidentified thrush [*Catharus* sp.]) were not nest predators. The Red-winged Blackbird, American Goldfinch, and Swamp Sparrow never attacked experimental clutches during experiments conducted near their active nests (J. Picman, unpubl. data). Photos of these species probably represent accidental visits. In the following analyses of temporal patterns of nest predation in different habitats we considered only the predatory species.

The rates of photographed nest visits by predators were highest in the forest, intermediate in the scrubland, and lowest in the marsh and old field (Table 2; $\chi^2 = 102.25$; df = 3; $P < 0.001$). The number of species of predators (avian, mammalian, or all combined) was highest in the

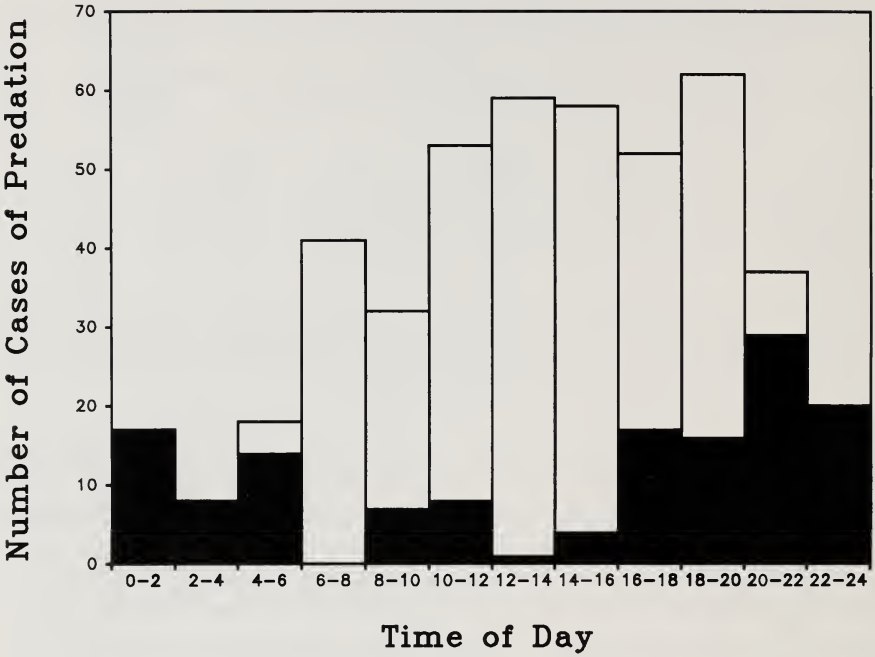

FIG. 1. The frequency of occurrence of predation as a function of time of day for all habitats combined. The black bars indicate the frequency of occurrence of mammalian predation. The avian predation is represented by open bars that were added on top of the black bars.

scrubland and forest habitats, intermediate in the old field, and lowest in the marsh (Table 2). However, in each of these habitats there were only one or two major (i.e., responsible for at least 10% of all cases of predation in a given habitat) nest predators (Table 2). Thus, with respect to the frequency of occurrence of predation events, each community of predators in our study areas was dominated by one or two species.

Mammalian predation (Fig. 1) was greatest between 20:00 and 22:00 h and was high between 16:00 and 06:00 h. Mammalian predation was infrequent between 06:00 and 16:00 h. In contrast, avian predation was high during the day and absent during the night (i.e., between 22:00 and 04:00 h). When the records of avian and mammalian predators were combined, there was a peak of predation between 10:00 and 20:00 h, evidently because of generally high avian predation at this time of day (Fig. 1).

Predation patterns in the four habitats varied significantly throughout the day for individual habitats (Table 3). In the marsh and old field, where predation patterns were similar in time, the highest proportion (50% and

TABLE 3

PREDATION[a] AS A FUNCTION OF TIME OF DAY IN THE MARSH, OLD FIELD, SCRUBLAND, AND FOREST

Habitat	22:00–04:00	04:00–10:00	10:00–16:00	16:00–22:00	Chi-square
Marsh	13/0 (13)[a]	5/1 (6)	5/0 (5)	24/0 (24)	19.17*
Old field	16/0 (16)	5/0 (5)	1/3 (4)	17/3 (20)	16.96*
Scrubland	2/0 (2)	4/23 (27)	3/26 (29)	8/42 (50)	42.89*
Forest	14/0 (14)	7/46 (53)	3/128 (131)	12/44 (56)	112.97*

[a] Mammalian/avian predation (total cases).
* P (two-tailed) < 0.001.

44%, respectively) of predation occurred late in the afternoon and in the evening. In the scrubland, however, predation was high throughout the day, with the peak between 16:00 and 22:00 h. In the forest, predation was generally high throughout the day and peaked between 10:00 and 16:00 h (Table 3).

Our data allowed closer examination of temporal patterns of nest predation by several species for which we had at least 20 records of the time of a predation event. Raccoons and striped skunks made most visits of experimental nests between 16:00 and 04:00 (Table 4), whereas Blue Jays were generally important throughout the day (i.e., between 04:00 and 22:00 h, Table 4). Unfortunately, for the remaining predators we did not obtain enough photos of predation events to be able to present a similar analysis of their predatory activity pattern throughout the 24-h cycle.

TABLE 4

THE TEMPORAL PATTERN OF PREDATION BY PREDATOR SPECIES FOR WHICH AT LEAST 30 RECORDS OF TIME OF THE PREDATION EVENT WERE OBTAINED

		Number of predation events that took place between:			
Predator	Habitat	22:00–04:00	04:00–10:00	10:00–16:00	16:00–22:00
Raccoon	Marsh	13	4	5	24
	Scrubland	1	3	1	1
	Forest	11	3	3	8
	Combined	25	10	9	33
Striped skunk	Old field	15	4	1	16
Blue Jay	Scrubland	0	21	21	40
	Forest	0	38	120	44
	All combined	0	59	141	84

DISCUSSION

Results of our camera study suggest that the cattail marsh had the lowest number of different types of predators, most likely because the deep water of the marsh prevented predators from effectively searching this habitat. Raccoon depredation, the single major cause of egg mortality in the marsh, was mostly in shallow marsh areas (Picman et al. 1993). Marsh Wrens (*Cistothorus palustris*) were absent during this study but are important nest predators when present (Picman et al. 1993). Because Marsh Wrens are diurnal, their presence could change the temporal pattern of predation activities in the marsh (Table 1). Composition of a predator community, and consequently the temporal pattern of predation in some habitats, may thus vary between years, depending on changes in the predator community.

In spite of the discovery that in some habitats up to nine predator species were recorded, each habitat had at most two major predator species. The presence of such a small number of major nest predators in each of the four habitats could be explained in several ways. First, it is possible that the "major" predators were highly mobile animals that could exploit the food source (experimental clutches) more effectively. Second, the "major" predators could have been nest specialists that are behaviorally more effective in searching for bird nests. Third, following the experimental increase in food (egg) availability, some predators may have specialized on this food source (i.e., exhibited the functional response). And fourth, the increased nest density in our study areas may have attracted more individuals of the "major" predator species (i.e., a predator may have exhibited a numerical response). Establishing the plausibility of the above explanations would require recognition of individual predators and data on their foraging behavior following the introduction of experimental clutches. In addition, we would also have to examine the effect of selective removals of the "major" predators on foraging activity of the "minor" predators. Such removal experiments should allow us to establish if the "minor" predators are generally less effective in finding nests or if their potential effects have been masked by increased (or more effective) foraging activity of the "major" predators.

The methods used in experimental predation studies are likely to affect predation patterns. For example, predation rates on eggs in artificial nests constructed from dry grass may differ from those on eggs in real nests (Storaas 1988, O'Reilly and Hannon 1989; but see Major 1990). The experimental approach could also affect the nest predation patterns because of the inability of observers to simulate the location of natural nests. Furthermore, frequent visits of experimental nests could attract predators,

thereby increasing predation rates on artificial clutches (but see MacIvor et al. 1990). Our results on the composition of predator communities in different habitats and the relative role of individual species of predators could have been influenced by our field methods and hence must be interpreted with caution. Specifically, our frequent visits of camera setups (once every day), creating disturbance, leaving scent paths leading to nests, and the use of camera setups which made the nests more conspicuous could have made it easier for at least some predators to find our experimental nests. On the other hand, the presence of human observers and camera setups might deter some predators, whose importance could thus be underestimated in our results. Unfortunately, we were unable to control for such effects and cannot establish their importance. However, because we used the same methods in all habitats, we believe that differences in predation that we observed between habitats, and at different times of day within individual habitats, are real.

Our data indicate that egg predation may occur at any time of day. Avian predators in our study area were exclusively diurnal, whereas mammalian predators exhibited the highest level of activity during late afternoon, evening and at night. The presence of avian and mammalian predators and their relative abundances seem to determine the temporal pattern of nest predation in different habitats. Thus, mostly mammalian predation in the marsh and old field habitats resulted in a predation peak characteristic of mammalian predators (i.e., late evening/night). In contrast, more frequent avian predation in the scrubland and forest resulted in more intense predation during the day (i.e., between 04:00 and 22:00 h) in these two habitats.

Our results on the temporal pattern of nest predation could have been influenced by the timing of our daily checks of the camera setups. Assuming high levels of predation, we should expect more predation soon after our checks of the camera transects when new eggs were placed in the experimental nests. Because all checks of camera transects were done between 9:00 and 12:00 h, the highest predation should occur early in the afternoon. In the forest, where predation was highest, 52% of all predation events occurred in the time period following the check (Table 3). This evidence supports the view that in the forest the timing of camera checks may have biased the data on the temporal pattern of predation events. In the scrubland, where predation was the second highest, only 27% of all predation events occurred immediately after the check. Therefore, in this habitat the timing of our camera transect checks did not seem to affect temporal patterns of predation. This is further supported by the observation that in the scrubland predation was highest between 16:00 and 22:00 h (Table 3). In contrast, where predation is generally low, and/

or where most predation occurs at night, we should expect little or no effect of our nest checks on temporal patterns of nest predation. This prediction is supported by data from the old field and marsh habitats, where only 9–10% of all predation events occurred during the time period following our check.

The belief that timing of our checks may have had different effects on the temporal pattern of predation in different habitats, depending on intensity of predation and types of predators present, is further supported by data on three most common predators, the raccoon, Blue Jay, and striped skunk, which occurred in habitats with different intensities of predation. In the forest (the highest predation; Table 1; J. Picman, unpubl. data), Blue Jays were the most important predator and caused most egg losses between 10:00 and 16:00 h; i.e., soon after our checks of camera transects (usually 09:00–12:00 h). This diurnal predator was responsible for almost 50% of all egg losses during our camera study. On the other hand, the temporal patterns of activities of raccoons and striped skunks (to a great extent nocturnal predators), which were important but a far less frequent cause of egg losses in their respective habitats (Table 4), do not seem to have been influenced by the timing of our checks of camera transects (Tables 1, 4).

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NESTING SUCCESS AND SURVIVAL OF VIRGINIA RAILS AND SORAS

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ABSTRACT.—Lack of estimates of nesting success and annual survival of North American rails limits our ability to monitor rail populations, regulate harvest levels, and institute recovery programs. We here present Virginia Rail (*Rallus limicola*) and Sora (*Porzana carolina*) population trends from Breeding Bird Surveys (BBS) throughout North America, estimates of nesting success from the Cornell Laboratory of Ornithology's Nest Record Program, and estimates of survival from radio-marked and banded birds in Arizona, 1985–1987. Virginia Rail populations declined 2.2% annually from 1982–1991, and Sora populations declined 3.3% annually from 1966–1991. Annual survival probability of radio-marked and banded Virginia Rails in Arizona was 0.526 ± 0.195 and 0.532 ± 0.128, respectively. Non-breeding survival probability did not differ between radio-marked Virginia Rails (0.545 ± 0.191) and Soras (0.308 ± 0.256) in Arizona. All documented mortality occurred between October and March for both Virginia Rails and Soras. Virginia Rail and Sora nesting success was 53%. Despite reproductive success and survival rates adequate for population maintenance, rail populations appear to have declined proportionately with continental wetland loss. *Received 24 Sept. 1993, accepted 20 Jan. 1994.*

Few studies have estimated reproductive success and annual survival of rails because they are secretive and attract little interest from hunters. Because wetland habitats have declined throughout the United States, information on population trends and life-history parameters is vital for determining whether populations of wetland-dependent species such as rails have suffered proportionately and are vulnerable to extirpation or extinction. Although Clapper Rail (*Rallus longirostris*), King Rail (*R. elegans*), Virginia Rail (*R. limicola*), and Sora (*Porzana carolina*) have liberal hunting regulations in many states, western taxa of Clapper Rail and Black Rail (*Laterallus jamaicensis*) are endangered. Nonetheless, few states monitor rail populations, and the effects of wetland destruction on rails have not been addressed. In addition, because few estimates of nesting success and annual survival of North American rails are available, our ability to monitor rail populations, regulate harvest levels, and institute recovery programs is limited. Effective management and conservation of rails requires identification of the environmental features affecting nesting success and survival.

In this paper, we present Virginia Rail and Sora population trends

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throughout North America from 1966–1991. We also estimate annual survival from radio-marked and banded birds in Arizona from 1985–1987 and nesting success, using nest record cards from throughout North America from 1920–1987.

METHODS

We examined Virginia Rail and Sora population trends (rates of annual change) in North America from 1966–1991, using North America Breeding Bird Survey (BBS) data from the U.S. Fish and Wildlife Service's (USFWS) Office of Migratory Bird Management. The Office of Migratory Bird Management has used route-regression analysis of BBS data to estimate population trends (Geissler and Noon 1981, Geissler and Sauer 1990) and bootstrapping (N = 400 repetitions) to estimate variances of trend estimates (Geissler and Noon 1981, Geissler and Sauer 1990). We examined 25-year (1966–1991) and 10-year trends (1982–1991) for both species, using weighted average numbers of birds tallied per BBS route (Robbins et al. 1980, Geissler and Sauer 1990). We present trends for Canada, the United States, North America, the Eastern region of North America (all States and Provinces east of the Mississippi River), the Central region (between the Rocky Mountains and the Mississippi River), and the Western region (west of the Mississippi River and north of Mexico, excluding Alaska). Sample sizes represent the number of BBS routes within the species' range that were conducted at least two years by the same observer during the time period.

In 1986 and 1987, we caught 88 Virginia Rails and 83 Soras in Yuma County, Arizona. Rails were captured with drop-door traps with lead fences and banded with USFWS aluminum bands. We radio-marked 42 of the 88 Virginia Rails and 26 of the 83 Soras. Radio transmitters weighing 3 g (Model MPB-1070-LD, Wildlife Materials, Inc., Carbondale, Ill.) were glued onto the backs of these birds. We monitored radio-marked birds from four fixed-tower, null-peak receiving stations for 1–6 h daily, six days/week. Tracking sessions were stratified so that each period of the day was represented, and birds were monitored during all four seasons. We obtained simultaneous azimuths from the two telemetry stations providing the best bearing intersection. Radio contact was never obtained on six Virginia Rails and three Soras, and these individuals were excluded from analyses. Loss of radio contact may have been a result of migrant departure, but at least one case was a result of radio failure. The mean duration of contact with radio-marked birds was 47.4 days (SD = 38.6) for 36 Virginia Rails and 24.6 days (SD = 15.6) for 20 Soras. Three Soras depredated within four days of capture were assumed to be a result of radio-marking and not used in survival analyses. Capture and telemetry techniques are described in further detail by Conway (1990) and Conway et al. (1993).

We calculated daily and interval survival probabilities for radio-marked Soras and Virginia Rails using MICROMORT version 1.3 (Heisey and Fuller 1985). Estimates of survival probability were for all age and sex classes combined because no valid sex criteria are available for rails, and because we had inadequate sample size for age groups. We calculated annual survival for Virginia Rails and non-breeding (August–April) survival for Soras because Soras migrated from our study area to breed elsewhere. We also calculated annual survival probability of banded Virginia Rails using Model D of the capture-recapture program JOLLY (Pollock et al. 1990). For JOLLY analyses, we divided capture histories into ten three-month capture periods. Goodness-of-fit tests were performed to confirm the adequacy ($\chi^2 = 26.92$, $P = 0.03$, df = 15) of Model D, which assumes constant survival and capture probability over the entire sample period (Pollock et al. 1990). JOLLY also calculates estimates of population size and capture probability. Sample sizes of banded birds were

TABLE 1

VIRGINIA RAIL AND SORA POPULATION TRENDS[a] FROM ROUTE-REGRESSION ANALYSES OF NORTH AMERICAN BREEDING BIRD SURVEY DATA FROM 1966–1991 (DROEGE 1990)

		1966–1991[b]			1982–1991		
Species	Region	Trend[a]	SD	N[c]	Trend	SD	N
Virginia Rail	Canada	0.2	0.6	37	−3.0	2.8	16
	United States	−0.4	0.6	142	−1.9[d]	0.8	77
	North America	−0.2	0.5	179	−2.2[d]	0.9	93
	East	0.2	0.6	96	0.4	1.8	44
	Central	−0.2	0.6	37	−3.6[e]	0.7	19
	West	−1.0	0.8	46	−3.3	2.9	30
Sora	Canada	−2.0	1.6	196	4.0	2.5	149
	United States	−9.9	6.1	332	−8.5[e]	2.1	241
	North America	−3.3[d]	1.7	528	1.6	2.2	390
	East	−0.6	0.6	169	0.4	2.4	102
	Central	−13.9[d]	6.3	136	−6.2[d]	2.7	108
	West	−0.6	1.1	223	3.0	2.7	180

[a] Percent change/year in abundance; data from USFWS, Office of Migratory Bird Management.
[b] Analyses began in 1966 in the east, 1967 for central regions, and 1968 in the west (Droege 1990).
[c] Number of BBS routes.
[d] Trend differs from 0.0 (Route-regression, $P < 0.05$).
[e] Trend differs from 0.0 (Route-regression, $P < 0.01$).

insufficient to calculate survival for Soras using JOLLY. We compared non-breeding survival probabilities between species and compared breeding and non-breeding survival probabilities for Virginia Rails using *z*-tests (Zar 1984).

We obtained 164 Virginia Rail and 203 Sora nest records from the Cornell Laboratory of Ornithology's Nest Record Program. We calculated nesting success using Mayfield's method (Mayfield 1961, 1975; Hensler and Nichols 1981) and compared estimates between species using *z*-tests (Zar 1984). Only 81 Virginia Rail and 108 Sora nest records were used for calculating nesting success because the Mayfield method requires that nests be visited ≥ two times. Mayfield estimates of nesting success assume constant survival throughout the nesting stage. Our small sample prevented us from validating that assumption. Nonetheless, Mayfield estimates are usually preferable to traditional ratio estimates of nesting success. Virginia Rail and Sora nest records were from 21 states and provinces (1920 to 1987), but 70% of Virginia Rail and 73% of Sora nest records were from the central U.S.

RESULTS

Virginia Rail populations were stable ($P > 0.10$, N = 179 BBS routes) from 1966–1991 but declined ($P < 0.05$, N = 93 BBS routes) 2.2 ± 0.9% annually from 1982–1991 in North America (Table 1, USFWS, unpubl. data). Sora populations declined ($P < 0.05$, N = 528 BBS routes) 3.3 ± 1.7% annually from 1966–1991 in North America (Table 1). From 1982–1991, Sora populations were stable ($P > 0.10$, N = 149 BBS routes) in Canada, but U.S. populations declined ($P < 0.01$, N = 241 BBS routes) 8.5 ± 2.1% annually (Table 1). Declines were most dramatic

in central North America (Table 1), where wetland loss has been most severe (Tiner 1984, Dahl 1990, Dahl and Johnson 1991).

Daily survival probability of radio-marked Soras in Arizona was 0.996 ± 0.003 and non-breeding (August–April) survival probability was 0.308 ± 0.256 for all age/sex classes combined. Daily survival probability of radio-marked Virginia Rails was 0.998 ± 0.001 and non-breeding survival probability was 0.545 ± 0.191 for all age/sex classes combined. Non-breeding survival probability did not differ ($z = 0.74$, $P = 0.23$) between species. Survival probability of Virginia Rails during the breeding season (1.00 ± 0.06) did not differ ($z = 0.04$, $P = 0.484$) from non-breeding survival probability, but all documented mortality (3 Virginia Rails and 2 Soras) occurred between October and March.

Because Virginia Rails were present throughout the year in Arizona and survival probability did not differ between seasons, we also calculated total daily and annual survival probabilities. Daily survival probability of radio-marked Virginia Rails was 0.998 ± 0.001 and annual survival probability was 0.526 ± 0.195 for all age/sex classes combined. Annual survival probability using capture-recapture was 0.532 ± 0.128 for all age/sex classes combined. Virginia Rail population size on our 112-ha study area was 54.5 ± 27.5 rails and probability of capture was 0.23 ± 0.04.

Daily nesting success (the daily probability of nest survival) for Virginia Rails throughout North America was 0.978 ± 0.005 (N = 81 nests). Over the 28-day nesting interval, overall nesting success was 0.530. Daily nesting success for Soras throughout North America was 0.978 ± 0.004 (N = 108 nests). Over the 28-day nesting interval, overall nesting success was 0.529.

DISCUSSION

The BBS is a roadside survey not specifically designed to monitor wetland birds (Gibbs and Melvin 1993), and only small numbers of rails are recorded along most BBS routes. The BBS prohibits eliciting responses from any species of birds, so encounters with rails on BBS routes were opportunistic. Location of roads influences estimates of relative abundance, and palustrine wetlands preferred by rails may be undersampled (Bystrak 1981, Robbins et al. 1986). Also, assessing the sensitivity of the BBS to detect population changes for species that have poorly understood life histories is difficult. However, patterns of population change detected from BBS data corroborate results of other independent surveys for other species (Droege 1990), and they may represent the best available data for evaluating long-term rail population trends.

Population trends from BBS data have a positive bias for species with low abundance (average count < 1.0) such as rails. Consequently, if a

species shows a significant negative trend, the trend is probably real and may be an underestimate of the actual trend (Geissler and Sauer 1990; B. Peterjohn, pers. comm.). Virginia Rail populations declined in North America during 1982–1991, and Sora populations plunged between 1966–1991, especially in the U.S. Declines were most apparent in the central U.S., where palustrine wetland loss has been particularly severe (Tiner 1984, Dahl 1990, Dahl and Johnson 1991). The 1982–1991 interval includes a national drought which began in 1980 (U.S. Fish and Wildlife Service 1986, 1988; Reynolds 1987), wherein many wetlands were dried naturally but not lost to agriculture or development. Hence, if water levels and precipitation return to normal levels, both wetlands and rail populations may recover. Palustrine wetland loss results in rail population declines (Eddleman et al. 1988), and consequently, habitat for rails has been diminished in both quality and quantity (U.S. Fish and Wildlife Service 1988).

We are unaware of any published estimates of survival probability for any species of rail. Our estimates of Virginia Rail survival are similar to those for other rallids. Annual survival of first and second year birds was 31% and 77%, respectively, for Common Moorhens (*Gallinula chloropus chloropus*) in West Germany (Cramp 1980) and 13–24% and 28–52%, respectively, for Eurasian Coots (*Fulica atra atra*) in northwest Europe (Cramp 1980). Annual survival of American Coot (*F. americana*) was 45% based on band-recovery data from western North America (Ryder 1963) and 43% and 21% for adult and juvenile birds in central North America (Burton 1959).

Non-breeding survival probability of Soras was low, compared to the species cited above, and may reflect increased mortality of radio-marked birds. For MICROMORT survival analyses, we assumed that loss of radio contact was statistically independent of death and minimized potential bias by obtaining frequent relocations on radio-marked birds (Heisey and Fuller 1985). Survival estimates of Virginia Rails were similar between MICROMORT and JOLLY estimates which used distinct subsets of individuals, lending support to the validity of our Virginia Rail estimates.

Although reported estimates of nesting success for rails are simple ratios of successful : total nests found, and hence are upwardly biased (Mayfield 1961, 1975), we compared our estimates to these because they are the only estimates available for rails. Our estimate of nesting success for Virginia Rails (0.53) is generally comparable to other estimates: 0.50 (8 nests) in Minnesota (Pospichal and Marshall 1954), 0.75 (24 nests) in Connecticut (Billard 1948), and 0.78 (27 nests) in Iowa (Tanner and Hendrickson 1954). Similarly, our estimate of nesting success for Soras (0.53) is generally comparable to others' estimates: 0.63 (16 nests) in Connect-

icut (Billard 1948), 0.61 (36 nests) in Michigan (Walkinshaw 1940), and 0.79 (34 nests) in Minnesota (Pospichal and Marshall 1954), but substantial variability does exist, even within sites. For example, Sora nesting success varied from 0.60 to 0.81 (50 nests) in two consecutive years in Alberta (Lowther 1977). Our estimates of nesting success for both species (0.53 and 0.53) are similar to 0.56 reported for California Clapper Rails (*R. l. obsoletus*) (Harvey 1988) and the 0.588 Mayfield estimate for Sandhill Cranes (*Grus canadensis pratensis*) in Florida (Dwyer and Tanner 1992) but lower than the 0.81 reported for Light-footed Clapper Rails (*R. l. levipes*) in California (Massey et al. 1984).

Virginia Rails are legally harvested in 37 states and Ontario, and bag limits are very liberal (25 birds/day in 35 states) (Conway and Eddleman 1994). Allowing such liberal bag limits without understanding the causes of population declines or estimates of nesting success and survival is not tenable. The USFWS has proposed the National Migratory Bird Harvest Information Program (NHIP) which would provide information on rail harvest and hunter pressure. Such a program is vital to proper rail management and monitoring and should be implemented immediately. Management agencies should either institute more effective harvest and population monitoring programs (e.g., NHIP) or reconsider rail harvest seasons until viable management programs are developed.

Rail population trends estimated from BBS data have shown declines. However, our results and previous studies suggest that rails have adequate reproductive success and survival for population maintenance/growth. Regional and continental rail population declines, if real, are best explained by loss of habitat. Rail populations appear to have suffered proportionately with continental wetland loss and should be monitored more effectively (Gibbs and Melvin 1993). The BBS does not adequately census rails. A more appropriate continent-wide survey (e.g., Gibbs and Melvin 1993) should be initiated immediately so that rail populations can be properly managed and conserved.

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MORE BIRDS NEST IN HYBRID COTTONWOOD TREES

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Abstract.—Natural hybrid zones can be centers of insect abundance and species richness. We investigated the possibility that this pattern may extend to other trophic levels. We found more bird nests in a cottonwood hybrid zone than in pure stands of *Populus fremontii* or *P. angustifolia*. Furthermore, within the hybrid zone, there were more nests in hybrid trees than in trees of either parental type. Differences in architecture between hybrids and the two parental species may account for these differences in nest distribution. Breeding bird surveys in each of the three zones showed no differences in overall abundance or diversity; however, there were significant differences among zones in the abundances of the most common species. Management of riparian areas should not overlook the importance of hybrid plants. *Received 25 May 1993, accepted 20 Nov. 1993.*

The role of habitat in structuring avian communities has been well studied. Complex habitats appear to support more species than simple ones; however, this complexity may be manifested in both the physical structure of the vegetation (physiognomy) and the plant taxonomic composition (floristics), and there is some debate as to which factor is more important (Rotenberry 1985). Studies that support the importance of physiognomy include MacArthur and MacArthur (1961), Willson (1974), and James and Wamer (1982), whereas Wiens (1969), Anderson and Shugart (1974), and Rice et al. (1984) emphasize the role of floristics. Here, we suggest that another factor, plant hybridization, may be an important component of habitat complexity, especially through its influence on nest site selection.

Riparian habitats support extremely high bird populations (Carothers et al. 1974, Szaro 1980, Knopf 1985). Over 50% of 166 species breeding in riparian areas of the Southwest are completely dependent on this habitat (Johnson et al. 1977). While several authors report that cottonwood stands contain the highest bird densities of riparian areas in western North America (Carothers et al. 1974, Johnson et al. 1977, Strong and Bock 1990), the potential role of hybrid trees has not been examined.

Hybridization in *Populus* is widespread and well documented (Eckenwalder 1984). We studied hybrids between Fremont (*P. fremontii*) and narrowleaf (*P. angustifolia*) cottonwood along the Weber River in northern Utah. Hybrids can be F_1's, which are intermediate between the two parental species, or backcrosses to *P. angustifolia* (Keim et al. 1989), producing a continuum of tree types. Fremont and narrowleaf cottonwood have quite different architectures and F_1 type hybrids make up another

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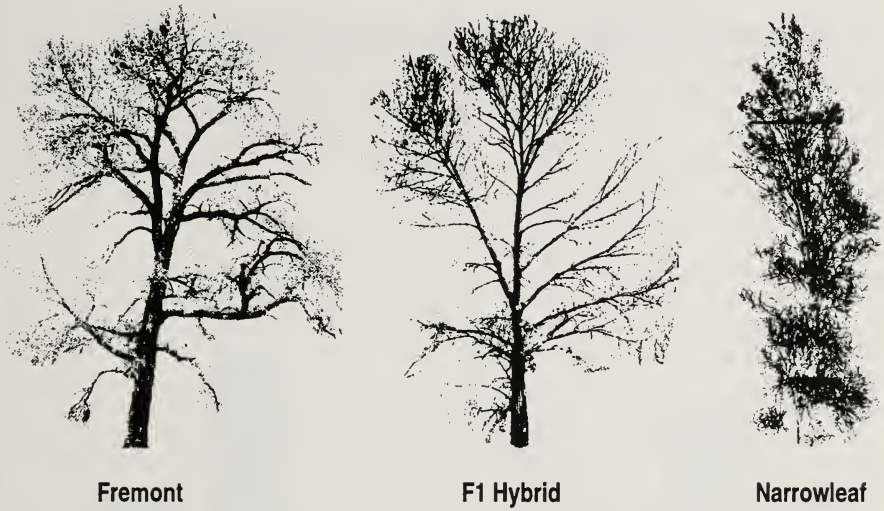

FIG. 1. There are three distinct categories of tree architectures: pure Fremont cottonwood, F_1 hybrid type (includes F_1 hybrids and close backcrosses), and narrowleaf cottonwood type (includes pure narrowleaf and complex backcross hybrids).

distinct architectural class (Fig. 1). The hybrid zone contains all of these tree types and is structurally more complex than the pure zones.

Hybrid zones can also be centers of insect species richness and abundance (Whitham et al. 1991), potentially increasing the resource base for insectivorous birds. For example, in the Weber River system, a dominant insect herbivore of cottonwood, the gall aphid *Pemphigus betae,* is often eaten by birds and is concentrated in the hybrid zone (Whitham 1989).

We investigated the possibility that birds respond to increased architectural complexity and insect abundances in the hybrid zone. We first examined patterns of nest distribution in pure stands of each cottonwood species and in the hybrid zone. Second, we looked at nest distributions among Fremont, narrowleaf, and F_1 type hybrid trees within the hybrid zone. Finally, we conducted breeding bird surveys to determine whether or not there are differences in avian communities among the three zones.

METHODS

Cottonwoods are the dominant tree throughout the drainage of the Weber River. Fremont cottonwood grows at elevations of approximately 1300–1500 m, and narrowleaf cottonwood grows at elevations of approximately 1400–2300 m. Where their ranges overlap, there is a 13 km long zone where extensive hybridization occurs. Complex backcross trees closely resembling pure narrowleaf cottonwood occur in the narrowleaf zone, but for the purposes of this study the hybrid zone was defined as the zone of overlap.

This research was conducted in the 13 km hybrid zone and in the adjacent (closest 5–8

km upstream and downstream) narrowleaf and Fremont zones. Thus, we were able to make comparisons among zones while also controlling for possible site differences not related to cottonwood trees. For example, several studies report different bird communities associated with different elevations (Knopf 1985, Strong and Bock 1990, Finch 1991). However, our lowest site (Fremont zone) was 1295 m, and our highest site (narrowleaf zone) was 1487 m, a difference of less than 200 m. Further, the only obvious habitat differences among zones are the different cottonwood tree phenotypes.

In early April 1991, before bud break, we surveyed trees for previous years' nests. The first survey compared nest densities among the three zones. At five sites in each zone, we examined the first 100 mature (>20 cm dbh) cottonwoods we encountered by walking along the river from west to east. We recorded numbers and species (if possible) of nests. The sites were matched for tree density as well as tree size. We looked at only living trees, so numbers of cavity nests were low.

The second survey compared nest densities on three groups of trees (Fremont architecture, narrowleaf architecture, and F_1 type hybrid architecture—see Fig. 1) within the hybrid zone. Backcross hybrids are common in the hybrid zone and their architecture closely resembles narrowleaf cottonwood. We surveyed 100 trees of each type for a total of 300 trees. Differences in nest densities were compared using χ^2 tests.

We conducted breeding bird censuses during late May and early June 1991. Birds were censused by direct count on fixed-width belt transects 200 m long and 100 m wide. We chose this length transect because it approximates the maximum length of relatively undisturbed mature cottonwood habitat along much of the Weber River. We censused five transects in each of the three zones. To determine if there were differences in the bird communities of Fremont, narrowleaf, and hybrid zone cottonwoods, we ran a MANOVA using the abundances of five common species: Black-billed Magpie (*Pica pica*), Northern Oriole (*Icterus galbula*), American Robin (*Turdus migratorius*), Yellow Warbler (*Dendroica petechia*), and Warbling Vireo (*Vireo gilvus*). We then used discriminant analysis to see if the distributions of these species would separate the transects into the three different zones.

RESULTS

There were almost three times as many bird nests in the hybrid zone as in either the Fremont or the narrowleaf zone ($\chi^2 = 53.09$, $P < 0.001$, Fig. 2A). The majority of these nests belonged to magpies and orioles, but we also found robin nests, several types of smaller cup nests, raptor nests, and some nest cavities.

Within the hybrid zone, we found twice the number of nests in cottonwood trees with the F_1 hybrid architecture as in either parental type ($\chi^2 = 13.58$, $P < 0.005$, Fig. 2B). The architecture of these hybrids is intermediate between that of the two species (Fig. 1). They may be more attractive as nest sites because they have both the relatively open crown of Fremont cottonwood and some of the fine branching of narrowleaf cottonwood.

Based on the abundances of the five common riparian species, there were significant differences in the bird communities of the hybrid zone, the Fremont zone, and the narrowleaf zone (Wilks' $\lambda = 0.063$, $P < 0.01$). The abundances of three of the five species were significantly different

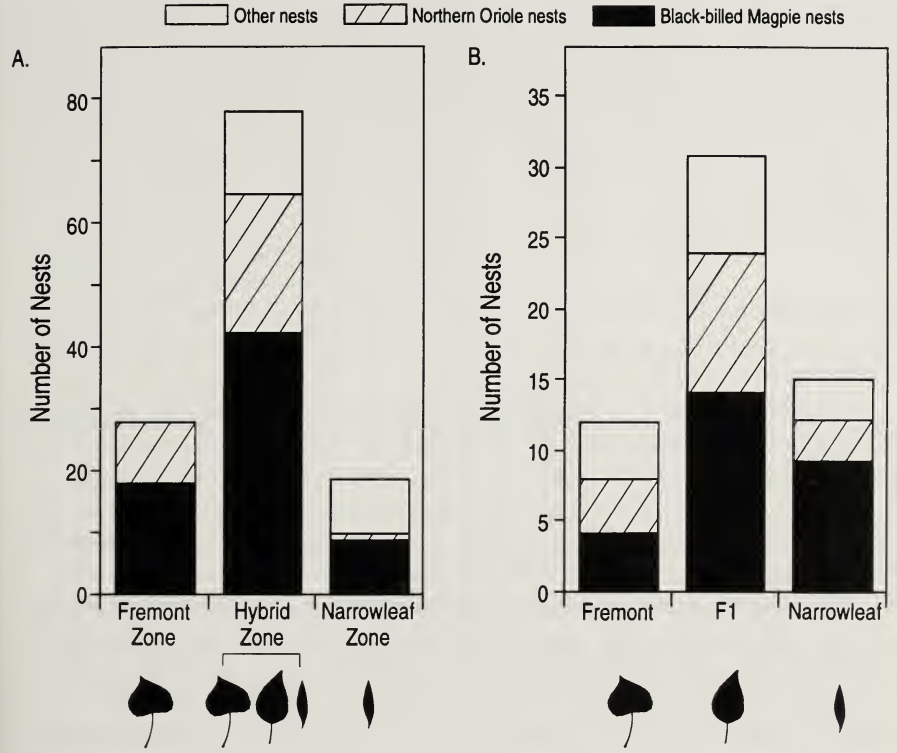

FIG. 2. A) Differences in nest distribution among the pure Fremont zone, the hybrid zone, and the pure narrowleaf zone (all nests: $\chi^2 = 53.09$, $P < 0.001$; magpie nests: $\chi^2 = 26.52$, $P < 0.001$; oriole nests: $\chi^2 = 22.16$, $P < 0.001$; N = 500 trees). B) Differences in nest distribution among tree types within the hybrid zone (all nests: $\chi^2 = 13.58$, $P < 0.005$; magpie nests: $\chi^2 = 6.1$, $P < 0.05$; oriole nests: $\chi^2 = 5.35$, $0.05 < P < 0.10$; N = 100 trees).

(Table 1). Magpies and orioles were clearly more abundant in the hybrid zone than in the narrowleaf zone, and orioles were slightly more common in the hybrid zone than in the Fremont zone. Also, discriminant analysis using bird species and abundance correctly classified 14 of the 15 transects as being either in the hybrid, Fremont, or narrowleaf zones.

DISCUSSION

Nest sites.—Genetically-different cottonwoods have very different architectures (Fig. 1), and our data suggest that birds respond to this physiognomic complexity by choosing to build nests in F_1 hybrids. We found more nests in the hybrid zone and more nests in F_1 hybrid trees within the hybrid zone. Because of their numerous lateral branches and associ-

TABLE 1

BREEDING BIRD CENSUS DATA AND RESULTS OF UNIVARIATE ANOVA'S FOR THE FIVE MOST COMMON SPECIES[a]

Zone		Black-billed Magpie	Northern Oriole	American Robin	Yellow Warbler	Warbling Vireo
Fremont	$\bar{x}$	5.4	2.0	6.6	3.2	0.55
	SE	0.51	0.71	1.53	1.16	0.24
Hybrid	$\bar{x}$	4.8	2.8	4.0	6.4	1.0
	SE	0.86	0.86	0.55	1.53	0.55
Narrowleaf	$\bar{x}$	0.6	0.4	5.0	13.6	3.2
	SE	0.4	0.24	1.18	1.50	0.80
ANOVA	*F*	17.69	3.45	1.27	14.28	5.88
	P	<0.001	0.066	0.316	0.001	0.017

[a] (MANOVA: Wilk's $\lambda = 0.063$; $P < 0.01$).

ated crotches, these hybrid trees may be better nest sites for some species of birds.

Other studies have emphasized the importance of nest site selection in driving avian abundance and species diversity. Martin and Roper (1988) proposed that Hermit Thrushes (*Catharus guttatus*) select habitats that contain many potential nest sites in order to reduce nest predation, and Martin (1988) argued that nest predation is important in organizing bird communities. Recently Steele (1993) tested the role of nest site selection versus foraging site selection and concluded that nest site requirements are probably more important.

Although the survey undoubtedly included nests of different ages, there is no reason to believe that nests would persist longer in the hybrid zone. How long nests stay in trees should be in large part a function of wind velocity. High winds are prevalent during much of the year throughout Weber Canyon, and the hybrid zone is located in one of the most exposed areas. Also, as cottonwoods are the dominant vegetation throughout this drainage, it is unlikely that we missed many nests located in other species of trees.

Foraging sites.—While our data indicate that nest site choice influences bird distributions in the hybrid zone, it is possible that some species are also responding to an abundant food resource. Rotenberry (1985) suggests that the most important source of variation among plants that birds are likely to respond to is the provision of food.

The cottonwood gall aphid, *Pemphigus betae,* is concentrated in the hybrid zone (Whitham 1989). Each gall contains up to 300 aphids, and a single tree has up to 50,000 galls (Whitham 1983). The galls mature in

June, so they become available at an important time for breeding birds. Rates of avian predation on these galls may be 25% or higher (Whitham 1987). We have observed Black-capped Chickadees (*Parus atricapillus*) opening galls and feeding on aphids (Whitham 1987). Other documented cases of birds preying on aphid galls include: Gila woodpecker (*Melanerpes uropygialis*; Speich and Radke [1975]), Tree Sparrow (*Passer montanus*; Sunose [1980]), and Great Tit (*Parus major*; Burnstein and Wool [1992]). Probably all of the species that we used for statistical analyses are capable of slicing open galls.

Conservation of hybrid plants.—Recent conservation policy has emphasized discouraging hybridization between species (O'Brien and Mayr 1991). This policy is based on studies of animal hybrids, where hybridization is thought to cause "genetic disintegration." However, hybridization in plants is important: an estimated 70% of angiosperms originated as interspecific or intergeneric hybrids (Stace 1987). And, as our data suggest, plant hybrid zones may provide unique habitat for different animal species.

The conservation of riparian areas, and specifically the importance of riparian habitats to birds, are issues that have recently received considerable attention (reviewed by Knopf et al. 1988). We propose that the value of riparian areas is augmented by the hybrid status of the riparian vegetation. Hybridization is common in both cottonwoods (Eckenwalder 1984) and willows (*Salix* sp.) (Brunsfeld et al. 1991), another native riparian plant. While hybrid zones occur in most drainage systems, they may be restricted to small areas (e.g., the cottonwood hybrid zone in Weber Canyon occupies only 13 km of the ca 500 km drainage of the Weber River). By providing better nesting habitat than either Fremont or narrowleaf cottonwood, this hybrid zone may influence avian community structure. For these reasons, we urge not only the conservation of riparian areas but the conservation of hybrid zones as well.

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WINTER MOVEMENTS AND SPRING MIGRATION OF AMERICAN WOODCOCK ALONG THE ATLANTIC COAST

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ABSTRACT.—Radio transmitters were attached to American Woodcock (*Scolopax minor*) at three Atlantic coastal sites to monitor winter movements and spring departure dates from Georgia (1982–1984, 1989–1991), South Carolina (1988–1989), and Virginia (1991–1992). There was no evidence of temperature, sex, or age-dependent migration dates. Migration was coincident with the full moon in February and the passage of weather fronts close to this time. *Received 13 Sept. 1993, accepted 1 Feb. 1994.*

Little is known about the spring migration of American Woodcock (*Scolopax minor*) other than that they generally leave wintering grounds beginning from late January to late February (Glasgow 1958, Pace and Wood 1979, Tappe et al. 1989, Olinde and Prickett 1991, Roberts 1993) and arrive on northern breeding grounds in late March and April (Sheldon 1971, Sepik et al. 1993). Initiation of spring migration may depend on temperature, with earlier departures during warmer winters and later departures during colder winters (Glasgow 1958, Martin et al. 1970, Roberts 1993), and may span several weeks at any one location (Roberts 1993). Moon phase, passage of weather fronts, day length, and reproductive state also may trigger the initiation of spring migration (Coon et al. 1976, Olinde and Prickett 1991). Sex-specific migration chronology has been alluded to, with males migrating earlier than females (Glasgow 1958, Martin et al. 1970, Owen 1977); however, both sexes appear to arrive at the breeding grounds simultaneously (Dwyer et al. 1988, Sepik et al. 1993).

All knowledge of woodcock spring migration is based on banding studies and anecdotal evidence. While this information is valuable, data obtained using radio telemetry is more reliable. During six winters between 1982 and 1991, we attached radio transmitters to woodcock at three wintering sites along the Atlantic coastal plain. We addressed three questions: (1) Does spring migration commence earlier during colder winters than during warmer winters?, (2) Is spring migration more variable during colder winters than during warmer winters?, and (3) Is there a difference between the spring departure dates by sex or age?

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STUDY AREA AND METHODS

We used three study sites along the lower Atlantic coastal plain. The first included the southern shore of the Altamaha River near Everett, Georgia, where the predominant habitat is timberland managed primarily for pulpwood. Pine (*Pinus* spp.) plantations were clear-cut, followed by intensive post-cutting management. The second study area was within the Francis Marion National Forest (FMNF) near McClellanville, South Carolina. This forest (100,000 ha) was 98% forested with about 75% in managed pines and the remaining 25% in bottomland hardwoods. The forest was managed intensively for timber production, using mostly clear-cutting, and enhancement of Red-cockaded Woodpecker (*Picoides borealis*) habitat. The third study area was the Eastern Shore of Virginia National Wildlife Refuge (ESVNWR) on the southern tip of the Delmarva Peninsula near Cape Charles, Virginia. It was agricultural fields scattered among older woodlots of mixed pines-hardwoods. Little forest management was evident in the area.

All three study areas were characterized by relatively mild winter weather. The mean number of days with the daily minimum temperature ≤0°C from December through February recorded at the weather stations closest to the study areas were: Norfolk, Virginia, 45 days; Pinopolis Dam, South Carolina, 37 days; Waycross, Georgia, 30 days (1951–1975; NOAA 1978). Soil temperatures at 10 cm depth were rarely <0°C (NOAA 1982–1992); any freezing of the soil at the surface was of short duration.

Study dates by site were (1) Georgia: 29 December 1982–3 March 1983; 14 December 1983–1 March 1984; 16 December 1989–15 February 1990; 28 December 1990–15 March 1991; (2) South Carolina: 14 December 1988–18 February 1989; and (3) Virginia: 9 December 1991–6 March 1992. Data were collected in Georgia during two studies: one during 1982–1984 (G. Haas, U.S. Fish Wildlife Service [USFWS], unpubl. data) and one during 1989–1991. The South Carolina study site was abandoned because of damage by Hurricane Hugo, and the Virginia study site was used only one winter. Due to the confounding of years and locations, any differences cannot be attributed only to year or location. Hereafter we refer to this combined effect as "year (location)."

Woodcock were captured using ground traps (Liscinsky and Bailey 1955), mist nets (Sheldon 1971), and nightlighting (Riefenberger and Kletzly 1967). They were banded with USFWS leg bands, weighed, aged, and sexed (Martin 1964, Mendall and Aldous 1943). A radio transmitter was attached to each bird dorsally between its wings, using a single multistrand wire loop harness and livestock tag cement (McAuley et al. 1993). Transmitters weighed 3.5–5.0 g, were attached to individual birds, and did not exceed 3% of body mass. This harness design does not inhibit normal behavior (McAuley et al. 1993). During every year, we tested 5% of the radios to determine if they met our specifications of ≥60 day life. In all years, all tested radios met this criterion.

During 1988–1992, we tried to capture 50 woodcock per year. Capture efforts continued until the sample size was obtained or until 31 January. Marked birds were tracked daily except during 14 February–15 March 1991 when locations were checked weekly, using vehicle-mounted four- or seven-element Yagi antennas. Once located, the status (alive, dead) of each bird was determined, using signal modulation. Woodcock classified as 'censored' included those birds whose fates were unknown, excluding birds which had died. If status could not be determined using signal modulation, the location of the bird was determined by approaching on foot for a visual sighting. The location of each bird was estimated to the nearest 50 × 50 m block. If a bird did not move within 48 h, we attempted to flush or recover it. We searched for lost birds from aircraft (Gilmer et al. 1981) within a 50-km radius of the center of the study area. If they could not be located from the air, we searched for lost birds from vehicles. Only censored birds are included in the present analyses.

A few woodcock were still present on the study areas when tracking was terminated. These birds were not included in the analyses because they may have been residents. We defined the migration date for each bird as the last day that the bird was located alive (censoring date). No birds censored before 16 January were included in these analyses, because birds disappearing before then probably were not permanently migrating (Glasgow 1958, Roberts 1993). We tested the effect of temperature on migration date by means of linear regression. We regressed the median censoring date by year against the mean daily minimum temperature spanning, either 15 December–5 February or 15 January–5 February, or against the average of the daily minimum temperature for the two weeks preceding each bird's censoring date.

Because spring migration may span several weeks at a given location (Roberts 1993), variation in spring migration may be weather-dependent. Weather could conceivably influence spring migration through the negative effect of cold temperatures on food availability. If food availability is more variable during colder years, then we hypothesize that variation in spring migration would be less in colder years because woodcock should not risk migrating when food availability to the north is questionable. That is, spring migration would be delayed until food availability is assured, and then all migrants would leave over a short time period. To test this hypothesis, we used linear regression to relate the standard deviation of censoring dates against the three temperature metrics mentioned above.

Use of censoring dates as an index of migration is not without fault as censoring can result from undetected death, temporary emigration, or radio failure. This could bias our analyses by suggesting that migration occurred earlier or in a different pattern than it did. This problem is important when censoring, unrelated to migration, varied among years (locations).

As a measure of winter severity, we used the mean daily minimum temperature (°C). We began the first mean at mid-December because, in most years, woodcock were present then at all sites (Pursglove 1975, Stamps and Doerr 1976), making this measurement representative of temperatures during the entire winter. Starting the mean at mid-January was much closer to when most woodcock migrated and might represent a late winter fine tuning of migration date. The final temperature measurement of the three is the most closely tied to the temperatures when birds actually were censored of the three measurements. We believe that daily minimum temperature is a relevant index to winter severity because earthworms (Lumbricidae), the primary food of woodcock (Cade 1985), are less available to woodcock during freezing temperatures (Reynolds et al. 1977, Stribling and Doerr 1985a).

Because year and location were confounded, we conducted two separate analyses. The first analysis used data from all six years, and the second, to avoid potential interaction among locations (latitude) and migration date, used only data collected in Georgia (four years).

We used a three-way ANOVA to test for the effects of sex, age, and year (location) on migration date. All interactions of the factors were included in the analysis. Analyses were conducted with all data and with Georgia data alone.

RESULTS

To address the use of censored birds as a measure of migration date, we evaluated several alternative explanations of censoring other than migration (see above). Undetected mortalities could have resulted from hunter kills not immediately reported. However, the only hunter kill reported to the USFWS Bird Banding Laboratory was a woodcock killed in the winter after it was marked, and only one hunter was encountered (several

times) during the study. Temporary movements could be a problem if those birds moved away from the study area but remained on the wintering grounds before beginning spring migration. During three winters (1988–1989, 1990–1991, 1991–1992), we documented five of 202 marked birds (2%) which moved from the study area, were not detected for ≥5 days during searches, and subsequently returned.

We did document marked birds permanently leaving the study area before the end of observations each year. These few woodcock remained near the study area for at least several days before being censored. One woodcock at Georgia 1982–1983 moved 14.5 km to the northwest along the Altamaha River. This bird remained at this location for two days and then was censored on 25 February 1983. One woodcock at Georgia in 1983–1984 moved 33.8 km to the northwest along the Altamaha River where it remained for one day and was censored on 8 February 1984. Three woodcock at South Carolina 1988–1989 began wandering northward from late December to mid-January. These birds moved between 2.9–3.6 km north across the Santee River before being censored in mid-February 1989. At Georgia 1990–1991, nine woodcock moved west around 29 January 1991 when the study area was flooded by the Altamaha River. These birds moved between 3.5–7.5 km before being censored: two in late January 1991 and seven in mid-February 1991. In Virginia in 1991–1992, one woodcock moved north 11 km and remained at that location for three days before being censored on 21 February 1992. Except for woodcock which were displaced by floodwaters in Georgia 1990–1991, the general pattern for migrating birds was a north to northwest movement ≥2 km. These birds remained at their new location for 1–3 days and then were censored. In no year or location did a woodcock move ≥2 km to the north or northwest and then return to the study area.

Median dates of censoring among years ranged from 1–22 February. The mean temperature for the entire winter ranged from 0.20–7.02°C, for the latter part of winter it ranged from −1.97–7.32°C, and for the average of the two weeks preceding censoring it ranged from −0.13–7.77°C. The coldest winter occurred in Virginia 1991–1992, while the warmest winter occurred in Georgia 1989–1990. All temperature measurements changed in the same direction between years, i.e., they all went up or down in unison, but due to temperature fluctuations within years, the measurements did not reflect one another in magnitude within years. For example, in 1982, the whole winter, late winter, and two-week mean temperatures reflected each other closely (3.30 vs 3.38 vs 3.39, respectively), whereas in 1983, the means did not (3.60 vs 5.15 vs 4.98, respectively).

Sample sizes by year and location were low in Georgia 1982–1983 and in South Carolina 1988–1989 but were adequate in all other years (lo-

TABLE 1

SAMPLE SIZES OF AMERICAN WOODCOCK WINTERING ALONG THE ATLANTIC COAST USED IN SPRING MIGRATION ANALYSES BY AGE, SEX AND YEAR (LOCATION)[a]

Year	Location	Young male	Young female	Adult male	Adult female
1982–1983	Georgia	8	3	2	1
1983–1984	Georgia	19	11	7	7
1988–1989	South Carolina	6	3	0	2
1989–1990	Georgia	21	8	5	4
1990–1991	Georgia	21	11	3	15
1991–1992	Virginia	21	17	2	5

[a] Because not all locations were represented every year, year (location) represents the confounding effects of year and location.

cations) (Table 1). No significant relationship ($P > 0.10$) was noted between median censoring date and any temperature measurement (Table 2, Fig. 1). All slopes were negative which was the expected direction. The direction of the slope was determined by Virginia 1991–1992 data when migration occurred late and temperatures were low. When only data from Georgia were analyzed, no significant relationships ($P > 0.10$) were

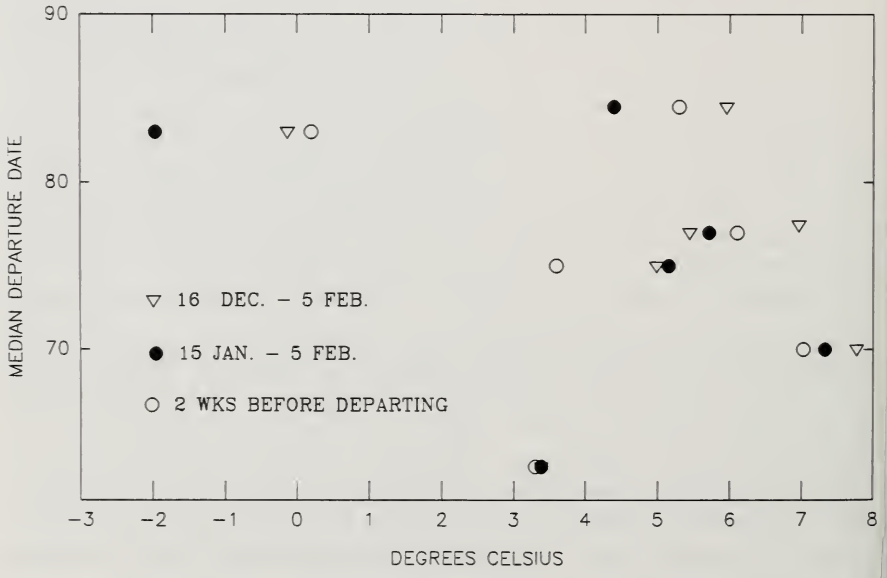

FIG. 1. Relationships between three winter temperature measurements and spring migration dates of American Woodcock wintering in coastal sites in Georgia, South Carolina, and Virginia between 1982 and 1991.

TABLE 2

RELATIONSHIP BETWEEN THREE WINTER TEMPERATURE MEASUREMENTS AND SPRING MIGRATION DATES OF AMERICAN WOODCOCK WINTERING ALONG THE ATLANTIC COAST FOR ALL SITES AND YEARS AND FOR GEORGIA

Response variable	Predictive equation	t^a	P
All sites and years			
MCD[b]	= 78.4 − 0.712 ($\bar{x}$ MDT[c] 15 Dec.–5 Feb.)	−0.44	0.68
MCD	= 79.3 − 0.968 ($\bar{x}$ MDT 15 Jan.–5 Feb.)	−0.83	0.45
MCD	= 78.5 − 0.670 ($\bar{x}$ MDT for 2 wks. before censoring date)	−0.46	0.67
SD MCD[d]	= 13.4 − 0.627 ($\bar{x}$ MDT 15 Dec.–5 Feb.)	−0.95	0.40
SD MCD	= 12.1 − 0.339 ($\bar{x}$ MDT 15 Jan.–5 Feb.)	−0.64	0.56
SD MCD	= 12.7 − 0.426 ($\bar{x}$ MDT for 2 wks. before censoring date)	−0.68	0.54
Georgia			
MCD	= 66.9 + 1.304 ($\bar{x}$ MDT 15 Dec.–5 Feb.)	0.36	0.75
MCD	= 71.6 + 0.298 ($\bar{x}$ MDT 15 Jan.–5 Feb.)	0.08	0.95
MCD	= 63.0 + 1.833 ($\bar{x}$ MDT for 2 wks. before censoring date)	0.57	0.63
SD MCD	= 20.7 − 1.848 ($\bar{x}$ MDT 15 Dec.–5 Feb.)	−2.14	0.17
SD MCD	= 23.4 − 2.278 ($\bar{x}$ MDT 15 Jan.–5 Feb.)	−46.54	<0.001
SD MCD	= 22.4 − 1.906 ($\bar{x}$ MDT for 2 wks. before censoring date)	−3.26	0.08

[a] t is for test of significance of slope ≠ 0.
[b] MCD = mean censoring data.
[c] MDT = minimum daily temperature.
[d] SD MCD = standard deviation of MCD.

evident (Table 2). Slopes were positive for the Georgia analyses although opposite of the expected direction. These slopes were indicative of the results obtained when the Virginia data were excluded.

Spring migration dates were variable across years, with Georgia 1982–1983 having the highest variability (SD = 15.76) and Georgia 1989–1990 had the lowest variability (SD = 6.72). No significant relationship ($P > 0.10$) was found between the standard deviation of censoring dates and any temperature measurement (Table 2). All slopes were negative which was opposite of the expected direction. Examining only data from Georgia revealed that no relationships ($P > 0.10$) were evident for the mean minimum temperature for the entire winter or the running mean temperature for two weeks preceding censoring, but a significant relationship ($P < 0.001$) existed for the minimum temperature for the late winter (Table 2). However, the slope was negative, opposite of the expected direction.

We found no effect of sex or age on spring migration dates (Table 3),

TABLE 3

RELATIONSHIP AMONG SEX, AGE, YEAR (LOCATION)[a] AND SPRING MIGRATION OF AMERICAN WOODCOCK

Source	df	MSE[b]	*F*	Pr > *F*
All sites and years				
Sex	1	0.664	0.00	0.95
Age	1	176.8	0.89	0.35
Year (location)	5	478.4	2.40	0.04
Sex*age	1	0.046	0.00	0.99
Age*year (location)	5	252.4	1.27	0.28
Sex*year (location)	5	128.8	0.65	0.66
Sex*age*year (location)	4	145.9	0.73	0.57
Error	179			
Georgia				
Sex	1	3.997	0.02	0.89
Age	1	74.19	0.37	0.54
Year	3	536.7	2.68	0.05
Sex*age	1	44.16	0.22	0.64
Age*year	3	348.3	1.74	0.16
Sex*year	3	154.7	0.77	0.51
Sex*age*year	3	116.5	0.58	0.63
Error	130			

[a] Because not all locations were represented every year, year (location) represents the confounded effects of year and location.
[b] MSE = Mean squared error.

although adults were poorly represented in all years (Table 1). An effect of year (location) was found with woodcock migrating significantly later from Virginia 1991–1992 and Georgia 1990–1991 than for the remaining years (locations) (SNK, $P = 0.05$). Using Georgia data, there was no effect of sex or age on spring migration dates (Table 3). Year was important, with woodcock leaving later during 1990–1991 than during other years (SNK, $P = 0.05$).

During two years (South Carolina 1988–1989, Georgia 1989–1990), there was a concentration of woodcock censored over a one-week period (Fig. 2). Coon et al. (1976) commented that fall migrating female woodcock departed shortly before a full moon. In both years, of those woodcock still present one week before the full moon in February, 90% in both South Carolina 1988–1989 and Georgia 1989–1990 were censored before the full moon. During the remaining four years, between 64–100% of the birds alive until one week before the full moon in February were censored within two weeks.

Coon et al. (1976) noted that fall migrating female woodcock generally

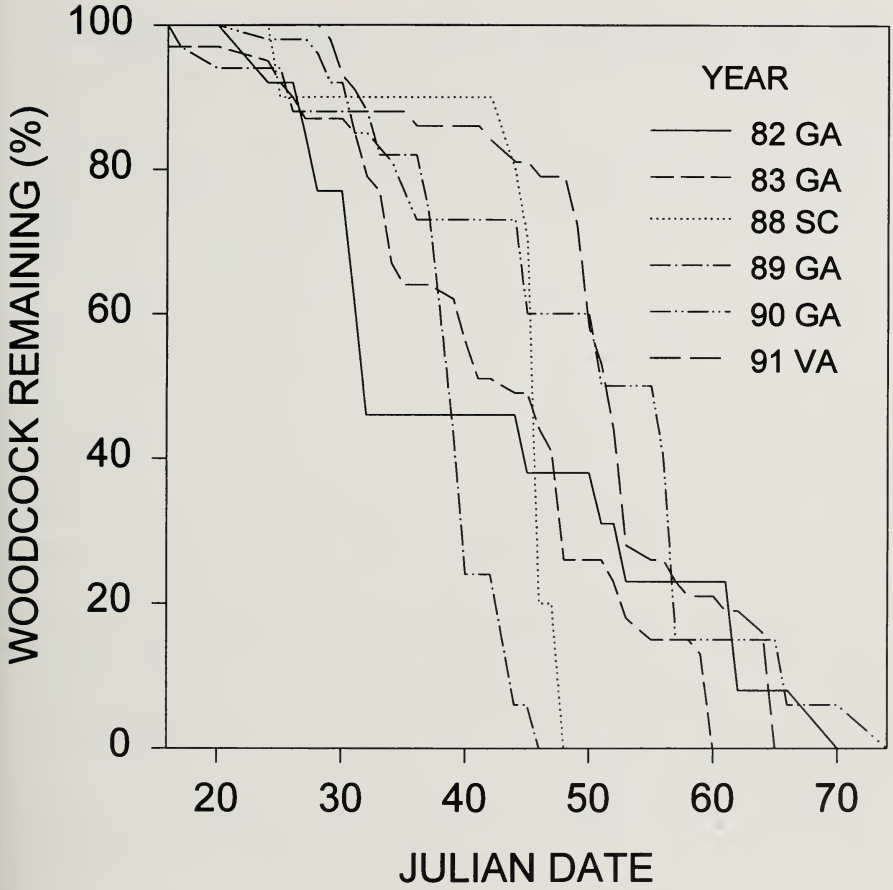

FIG. 2. Censoring dates for American Woodcock during spring migration from coastal sites in Georgia, South Carolina, and Virginia between 1982 and 1991.

departed when cold fronts approached and winds blew from the northwest. We, too, found that the passage of fronts was coincident with ≥ five woodcock departing in different years. Excluding Georgia 1982–1983, when no more than two birds per day were censored, concentrations of woodcock were censored <24 h after a front passed and the wind blew from the south or southwest (NOAA 1982–1992). Further, in the three years noted above, when a large percentage of the remaining woodcock were censored over a short period, during the two weeks around the full moon, northerly winds blew for about 65% of the time while winds from the south or southwest occurred only for about 20% of the time (NOAA

1982–1992). The birds moved when the wind blew from a southerly direction.

DISCUSSION

The reasons that woodcock initiate spring migration are probably many but likely include the advantages of arriving early at the breeding grounds (Sheldon 1971, Sepik et al. 1993), access to increased food resources (Gauthreaux 1982), and increased survivorship (Greenberg 1980). The mechanisms triggering migration in woodcock include photoperiod, weather, and possibly reproductive state (Coon et al. 1976, Olinde and Prickett 1991, Roberts 1993). Based on our analyses, mean minimum temperatures during the winter were not related to spring departure. Although we found no relationship between winter temperatures and spring migration, we do advise some caution with this interpretation because of the small sample size. We calculated the power to detect a correlation with six or four years of data and a true correlation of 0.1; the observed correlations were <10%. Estimated powers were 13 and 12%, respectively.

The apparent absence of temperature dependent migration and the coincidence between censoring and the moon phase suggested that migration is fairly constant among years. Such consistency agrees with the observation that on the Maine breeding grounds, woodcock arrive each year on about the same date (Dwyer et al. 1988, Sepik et al. 1993, but see Mendall and Aldous 1943).

Variability in the migration dates within a year was great and was related to late winter temperatures in Georgia. Apparently warmer temperatures concentrate the departure of migrating woodcock but not necessarily towards earlier dates. Again we are somewhat hesitant in drawing this conclusion because only one of six regressions demonstrated a significant relationship, although all slopes were negative.

The notion that spring migration is sex- or age-specific was not supported. We believe that the apparent disparate migration of woodcock by sex or age results from misinterpreting banding data as has been suggested previously (Stribling and Doerr 1985b, Diefenbach et al. 1990, Sepik et al. 1993). Female woodcock tend not to frequent nocturnal roosting fields at the same rate or possibly in the same location as males (Owen and Morgan 1975, Horton and Causey 1979, Stribling and Doerr 1985a, Sepik et al. 1993). Because most capture methods rely on capturing woodcock on roosting fields, the potential for a biased sample ensues.

We did find an association between spring departure and both moon phase and the passage of weather fronts. The association between spring departure and the full moon is intriguing because of the reluctance by

wintering woodcock to enter or remain in nocturnal fields around the time of the full moon (Glasgow 1958; USFWS, unpubl. data). Possibly the concern over nocturnal predators (Dunford and Owen 1973) is superseded by the aid of moonlight in navigating. The association between migration and the passage of weather fronts has been noted in other species (Gauthreaux 1982). The movement of weather fronts and the switch in the wind direction provided beneficial conditions which triggered or "released" woodcock to migrate (Coon et al. 1976).

Sheldon (1971) and Owen (1977) hypothesized that woodcock usually undergo partial migrations in response to winter temperatures. Accordingly, woodcock remain as far north as the temperatures allow at the beginning of the winter and move southward in response to declining temperatures. Whether woodcock return to their previous locations after temperatures ameliorate is not clear (Owen 1977). Exceptions to these partial migrations in response to cold temperatures do occur, as Sheldon (1971) and Mendall and Aldous (1943) noted that large numbers of woodcock sometimes die during cold weather rather than migrate southward. Our data spanned six years between 1982 and 1992, and within each winter, ≤ five woodcock per day were censored at any time between mid-December and the first week in February (unpubl. data). This pattern held true even in the last week of December 1989 when a severe cold front moved into Georgia, reducing the daily temperature to below freezing for one week and was accompanied by a rare snowfall. The pattern of censoring within the years we examined was not indicative of partial migration, i.e., once woodcock arrived at their coastal wintering site, they remained there until spring migration.

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BODY MASS AND COMPOSITION OF RING-NECKED DUCKS WINTERING IN SOUTHERN FLORIDA

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ABSTRACT.—We studied effects of sex, age, and date on body mass and composition of Ring-necked Ducks (*Aythya collaris,* hereafter Ring-necks) in southern Florida in winter 1979–1980. We conducted this analysis to assess the potential influence of dominance relations among sex-age classes on nutrient acquisition and to elucidate factors influencing patterns of change in body mass and composition of diving ducks in winter. Size-adjusted body mass (ADJMASS) was greater in adult than in immature Ring-necks, but ADJMASS of all birds increased during winter. Body fat (FAT) also increased through the winter but, unlike ADJMASS, was not affected by age. Size-adjusted protein (ADJPROT) varied by age and by sex and date. ADJPROT was greater in adults than in immatures. ADJPROT remained unchanged in females and increased (14%) in males, but sex-related differences averaged less than 2% for the entire winter period. Size-adjusted leg mass (ADJLEG, an index of feeding activity) increased through winter in immatures only and was equivalent in adults and immatures by late winter. Changes in ADJLEG and FAT were positively related, suggesting that Ring-necks gained fat through increased feeding. This relation (our measure of feeding efficiency) was not affected by sex or date, but the relation between ADJLEG and FAT was influenced by age. We found limited evidence that dominance relations influenced nutrient acquisition by Ring-necks in Florida during the year of study. Patterns of change in winter body mass and composition of Ring-necks and other diving ducks vary geographically. We argue that local environmental conditions, especially ambient temperature and food availability, are proximately responsible for observed variation. We further suggest that geographic differences are ultimately related to waterfowl mating systems. *Received 23 Sept. 1993, accepted 17 Dec. 1993.*

Body mass and composition of waterfowl (Anatidae) change substantially in winter. Many species exhibit midwinter declines in mass or composition (e.g., Canada Goose [*Branta canadensis*] [Raveling 1979]; Oldsquaw [*Clangula hyemalis*] [Peterson and Ellarson 1979]; Green-winged Teal [*Anas crecca*] [Baldassarre et al. 1986]; Northern Pintail [*A. acuta*] [Miller 1986]; Blue-winged Teal [*A. discors*] [Thompson and Baldassarre 1990]). The extent of mass loss varies among species and within species by latitude, social status, sex, age, and year (e.g., Paulus 1980, Thompson and Baldassarre 1990). Nonetheless, similarities in patterns of change during winter have led some investigators to speculate that body mass was endogenously controlled (Reinecke et al. 1982, Baldassarre et al. 1986, Perry et al. 1986, Thompson and Baldassarre 1990). Changes in body masses of wintering diving ducks (Tribe Aythyini) do not show

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declines consistently. Diving ducks wintering in New York, Chesapeake Bay, and coastal North Carolina show midwinter declines in body mass (Kaminsky and Ryan 1981, Perry et al. 1986, Lovvorn 1987), but Canvasbacks (*Aythya valisineria*), Redheads (*A. americana*), and Ring-necked Ducks (*A. collaris,* hereafter Ring-necks) in the Gulf of Mexico gain weight through winter (Jeske 1985, Hohman et al. 1988, Moore 1991, Hohman 1993).

In coastal South Carolina, dominance relations among wintering Ring-necks influenced access to limited food resources (Alexander 1987). Alexander (1987) determined adults to be dominant to immatures within sexes and, between sexes, males to be dominant to females. Alexander (1983) suggested that male dominance was responsible for sexual differences in winter distributions of Ring-necks (males wintering farther north than females). Similarly, Nichols and Haramis (1980) argued that male dominance was responsible for sexual differences in winter distribution, location within flocks, and habitat use of Canvasbacks. Competition between the sexes and age classes during winter is assumed to be deleterious to females and immatures; however, effects of competition on survival and reproductive performance (or correlates thereof) have not been demonstrated (Hohman 1993).

Here we examine the influence of sex, age, and date on body mass and composition of wintering Ring-necks in southern Florida. We conducted this analysis in part to assess the potential influence of dominance relations on nutrient acquisition by Ring-necks. Specifically, we tested the predictions that (1) mass and composition of subordinates (females, immatures) were different from those of dominants (males, adults) and (2) that subordinates fed less efficiently than dominants. Results from this study were interpreted in the context of similar studies and used to elucidate factors influencing patterns of change in body mass and composition of diving ducks in winter.

STUDY AREAS AND METHODS

This study was conducted at the Arthur R. Miller Loxahatchee National Wildlife Refuge (Loxahatchee NWR), a 60,000-ha impoundment located in Florida's northern Everglades (see Maffei [1991] for site description). Waterfowl hunting was permitted (morning only) on approximately 25% of Loxahatchee NWR, 22 November 1979 to 20 January 1980. Foods were rarely found in the esophagi of birds killed before 12:00 h (Hohman 1984). To minimize interference with hunting and increase our sample of birds with foods in their esophagi, we shot birds in the evening (>16:00 h) as they returned to roosting areas within or adjacent to the sanctuary portion of Loxahatchee NWR.

Measurements taken in the field included body mass (±5 g), bill length from the commissural point to tip of nail (±0.1 mm), maximum bill width distal to nares (±0.1 mm), keel length (±0.1 mm), tarsal bone length (±0.1 mm), and body length measured from the tip of the bill to the base of the middle rectrix (±0.5 cm) with the bird on its back. Birds

were categorized as hatch-year (immature) or after-hatch-year (adult) based on plumage (Hohman and Cypher 1986) or cloacal characteristics (Hochbaum 1942).

Carcasses were sheared to remove feathers (cf. Raveling 1979). Skin (including all associated fat) and omental fat were excised and weighed (±0.01 g). After the eviscerated carcass was weighed (±0.01 g), the right leg (masses of femur and tibiotarsus bones and all muscles having either origin or insertion on the femur or tibiotarsus) was excised and weighed (±0.01 g). The combined mass of skin and omental fat was positively correlated with total body fat ($r^2 = 0.96$; $P < 0.001$), and the eviscerated carcass was positively related to ash-free lean dry mass of Ring-necks ($r^2 = 0.69$, $P < 0.001$; Hohman and Taylor 1986). Consequently, we used the sum of skin and omental fat masses and eviscerated carcass mass as indexes of body fat (FAT) and protein (PROTEIN), respectively.

We examined the influence of sex, age, and date (1 November = day 1; 28 February = day 120) on body mass and composition of Ring-necks by using analysis of covariance models with type III sums of squares (PROC GLM, SAS Instit., Inc. 1987). First, we subjected the correlation matrix of five structural measurements (tarsus, keel, bill, body length, and bill width) to principal components analysis (PROC PRINCOMP, SAS for calculations). To characterize size of Florida Ring-necks more accurately, we included, in this analysis only, 27 birds collected in west central Florida, winter 1979–1980 (Hohman 1984). The first principal component accounted for 61% of the variance in the original measures, described positive covariation among all measurements, and had loadings ranging from 0.39 to 0.48. We used scores along the first principal component as a measure of body size (SIZE) and, therefore, as a covariate in analyses of factors affecting body mass, FAT, PROTEIN, and leg mass (LEG) (Ankney and Alisauskas 1991). Analysis of variance was used to test for effects of sex, age, and date on SIZE (PROC GLM, SAS Instit., Inc. 1987).

To test for sex- and age-related differences in foraging efficiencies of Ring-necks (here defined as fat accumulation relative to an index of locomotory effort), we examined relations between FAT and LEG. We assumed that changes in LEG were related to level of locomotory or foraging activity as in molting Canada Geese (Hanson 1962). Examination of sex and age effects on the relation between FAT and LEG was possible because Ring-neck diets (esophageal contents only) contained >98% plant material (almost exclusively seeds of white water-lily [*Nymphaea odorata*]) and did not vary among sex-age classes or months (Weller, unpubl. data). LEG was related to SIZE as follows:

$$\text{LEG} = 25.94 + 0.651(\text{SIZE}),$$
$$\text{df} = 175, \quad r^2 = 0.220, \quad P < 0.001.$$

Following Ankney and Alisauskas (1991:801), we used residuals from this regression to calculate size-adjusted values of LEG (ADJLEG) for Ring-necks. Analysis of covariance with type I sums of squares was used to test for heterogeneity of slopes (SAS Instit., Inc. 1991:229–246; Model: FAT = ADJLEG, date, sex, age, and all interactions). Factors not contributing significantly to the model were removed in a stepwise manner. Significance level was set a priori at $P = 0.05$.

RESULTS

We collected 177 Ring-necks at Loxahatchee NWR between 9 November 1979 and 28 February 1980. Our sample included 85 males (40 adults, 45 immatures) and 92 females (57 adults, 35 immatures). Males were structurally larger than females, and adults were larger than immatures, but SIZE was not affected by date or any interactions (Table 1, Appendix I). Size-adjusted body mass (ADJMASS) was greater in adult than in

TABLE 1

SIZE, SIZE-ADJUSTED BODY MASS (ADJMASS) AND PROTEIN (ADJPROT) OF RING-NECKED DUCKS COLLECTED IN FLORIDA, WINTER 1979–1980

Variable	N	Size[a]	ADJMASS (g)	ADJPROT (g)
Sex				
Male	85	1.30 (0.13)[b]		347.1 (2.8)
Female	92	−1.26 (0.13)		342.0 (2.7)
Age				
Adult	97	0.42 (0.13)	713.7 (4.5)	353.0 (2.2)
Immature	80	−0.37 (0.14)	685.6 (4.8)	336.1 (2.3)

[a] Size = scores along the first principal component: a linear combination of five structural measurements based on their correlation matrix.

[b] Least squares mean (SE) based only on factors contributing significantly to model.

immature Ring-necks (Table 1), but ADJMASS of all birds increased through winter (Fig. 1, Appendix I). FAT also increased through winter (Fig. 1), but, unlike ADJMASS, was not affected by age (Appendix I).

Size-adjusted protein (ADJPROT) varied by age and by sex, and date (Appendix II). ADJPROT was greater in adults than in immatures (Table 1). Whereas ADJPROT remained unchanged in females through the winter, it increased (14%) in males (Fig. 2).

Size-adjusted leg mass increased through the winter in immatures only and was equivalent in adults and immatures by late winter (Fig. 2, Appendix II). ADJLEG was positively related to FAT ($F = 27.95$, df = 1, 161, $P < 0.001$). Interactions between sex and/or date and ADJLEG were nonsignificant (F's = 0.09–1.40, df = 1, 161, P's > 0.239), but relations between ADJLEG and FAT were affected by age ($F = 3.91$, df = 1, 161, $P = 0.049$). Increases in FAT per unit measure of foraging effort (i.e., ADJLEG [g]) were greater in immatures than in adults (Fig. 3).

DISCUSSION

Influence of dominance relations on nutrient acquisition.—The potential for defense of feeding sites by diving ducks exists whenever food is

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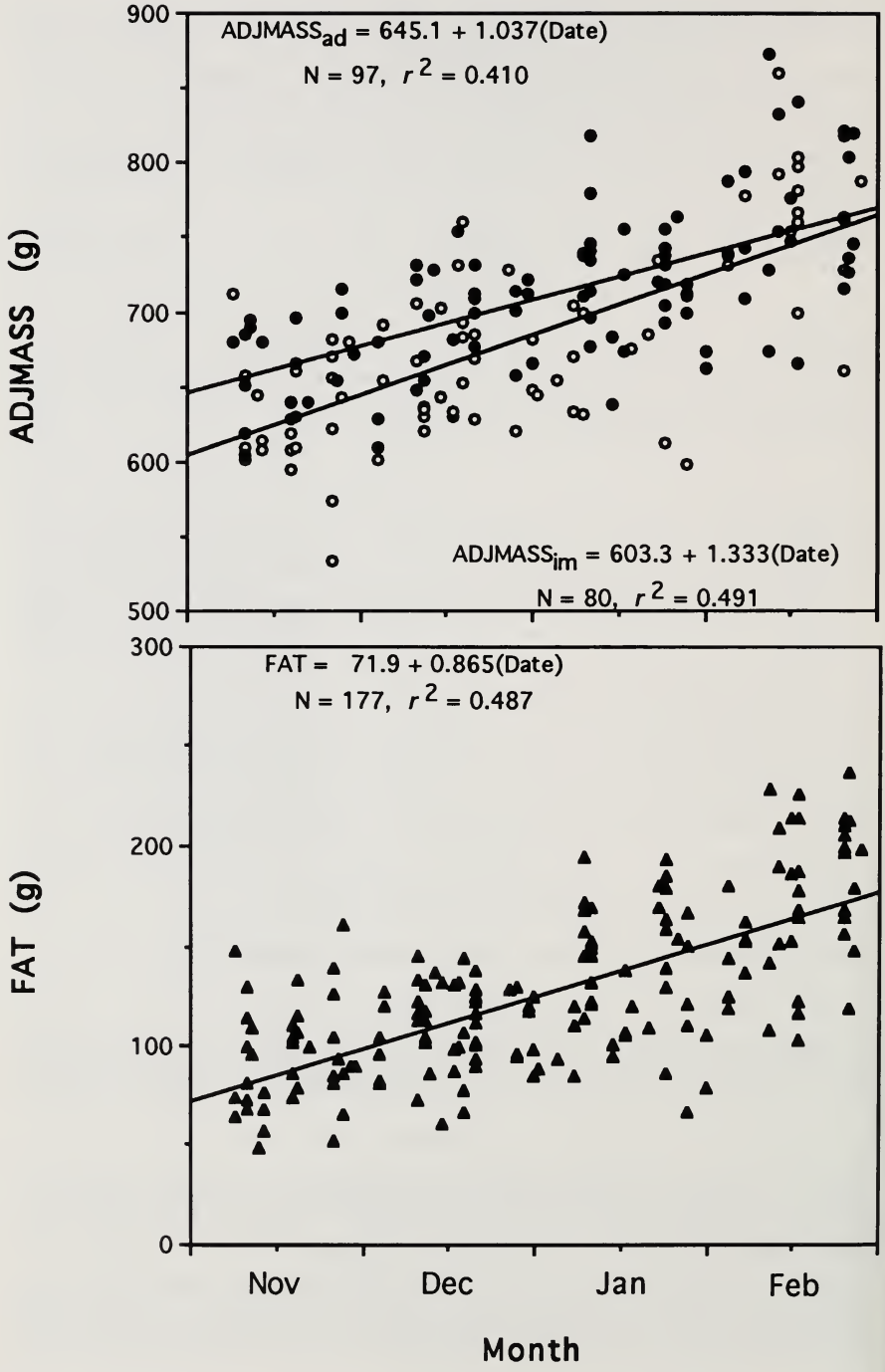
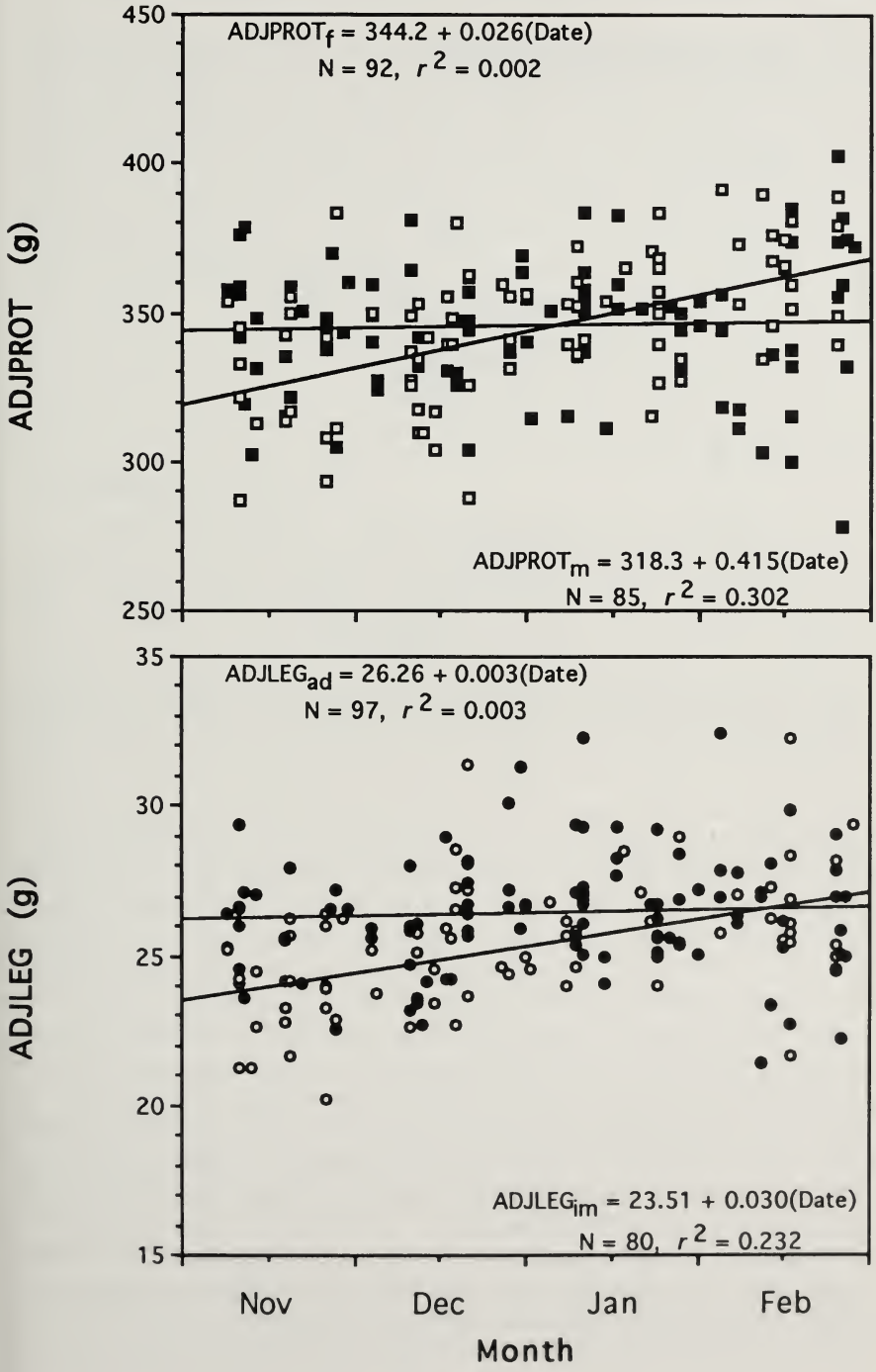
FIG. 1. Changes in size-adjusted body mass (ADJMASS) and fat of Ring-necked Ducks collected in southern Florida in winter 1979–1980. Date: 1 November = day 1. Adult (solid circle), immature (open circle), and combined (solid triangle).

FIG. 2. Changes in size-adjusted protein (ADJPROT) and leg mass (ADJLEG) of Ring-necked Ducks collected in southern Florida in winter 1979–1980. Date: 1 November = day 1. Adult (solid circle), immature (open circle), male (open square), and female (solid square).


ADJMASS (g)
900
800
700
600
500
ADJMASS$_{ad}$ = 645.1 + 1.037(Date)
N = 97, r^2 = 0.410
ADJMASS$_{im}$ = 603.3 + 1.333(Date)
N = 80, r^2 = 0.491
FAT (g)
300
200
100
0
FAT = 71.9 + 0.865(Date)
N = 177, r^2 = 0.487
Nov
Dec
Jan
Feb
Month


ADJPROT (g)
450
400
350
300
250
ADJPROT$_f$ = 344.2 + 0.026(Date)
N = 92, r^2 = 0.002
ADJPROT$_m$ = 318.3 + 0.415(Date)
N = 85, r^2 = 0.302
ADJLEG (g)
35
30
25
20
15
ADJLEG$_{ad}$ = 26.26 + 0.003(Date)
N = 97, r^2 = 0.003
ADJLEG$_{im}$ = 23.51 + 0.030(Date)
N = 80, r^2 = 0.232
Nov
Dec
Jan
Feb
Month

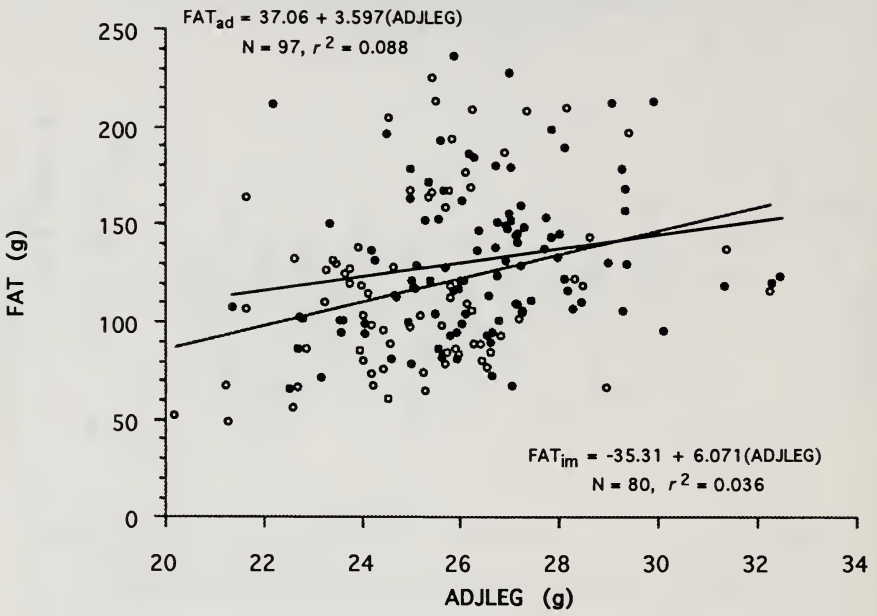


FIG. 3. Relation of body fat (FAT) to size-adjusted leg mass (ADJLEG) of adult (solid circle) and immature (open circle) Ring-necked Ducks collected in southern Florida in winter 1979–1980.

appropriately distributed (cf. Lovvorn 1989). In coastal South Carolina, where birds fed on tubers of banana water-lily (*Nymphaea mexicana*), site defense by diving ducks was favored by shallow water depth, irregular distribution of foods, substantial investments of time and energy required to excavate tubers, and high nutritional value of tubers (Alexander 1987). We believe that the potential for site defense by wintering Ring-necks also existed in southern Florida. There, Ring-necks fed diurnally on seeds of white water-lily in water depths less than 1.5 m (Weller, unpubl. data). They probably located submersed flower heads visually and fed on flower heads before seed dispersal. This interpretation was supported by large food volumes found in esophagi (i.e., high rates of ingestion) and presence of immature seeds and miscellaneous flower head fragments in food samples (Hohman 1984). Although we have no data on the distribution or abundance of water-lily flower heads, we believe that considerable search time was required to find submersed flower heads and that, once located, flower heads represented defendable resources.

In spite of the likelihood of site defense and potential asymmetries in

social interactions related to size differences between sex-age classes, there was limited evidence in our data to indicate that nutrient acquisition by wintering Ring-necks was influenced by dominance relations during the year of study. Sex had little or no effect on body mass and composition of Ring-necks wintering in southern Florida. ADJMASS and FAT changed similarly in males and females. ADJPROT was affected by sex, remaining constant in females and increasing (14%) in males; however, differences between sexes averaged less than 2% for the entire winter period (Table 1). Speculation that adults interfered with feeding by immatures was supported by our finding that immatures were lighter and had less ADJPROT than adults; however, we found no evidence of age-related differences in FAT or late-winter ADJMASS and ADJLEG of Ring-necks. Moreover, agonistic behavior among wintering Ring-necks at two nearby sites in central Florida was rarely observed (Hohman 1984, Jeske 1985).

Likewise, there was no indication that females or immatures fed less efficiently than males or adults. Assuming that changes in ADJLEG were related to locomotory (primarily feeding) activity, the positive association between ADJLEG and FAT suggested that Ring-necks gained fat through increased feeding. This relation was not influenced by sex, which we interpret to indicate that males and females fed with the same efficiency. However, feeding efficiencies of adult and immature Ring-necks apparently differed. ADJLEG explained less than 9% of the variation in FAT of immatures or adults, but, contrary to prediction, fat gained per measure of foraging effort (ADJLEG) was greater for immatures than adults. Age-related differences in foraging efficiency were not related to diet because adults and immatures selected the same foods (Weller, unpubl. data). We are unable to explain apparent differences in feeding efficiencies of adults and immatures, but we are confident in our conclusion that adults did not interfere with nutrient acquisition by immatures.

Proximate and ultimate controls of body mass and composition.—Patterns of change in body mass and composition of diving ducks during winter vary geographically. Ring-necks and other diving ducks in the Gulf of Mexico region gain body mass during winter, whereas diving ducks wintering at more northerly sites exhibit midwinter declines in body mass. Midwinter declines in body mass, feed intake, and activity of captive Canvasbacks fed ad libitum rations led Perry et al. (1986) to speculate that body mass of Canvasbacks was endogenously controlled. They argued that these changes increased the probability of survival in ducks by decreasing maintenance energy costs during periods of cold stress. However, geographic variation in body mass changes of diving ducks during winter does not support their argument for endogenous control. We be-

lieve that local environmental conditions, especially ambient temperature and food availability, are proximately responsible for observed geographic variation. Declines in body masses of Canvasbacks and Redheads wintering in New York from January to March were attributed to increased thermoregulatory costs and reduced food availability (Ryan 1972, Kaminsky and Ryan 1981). Canvasbacks wintering in coastal North Carolina (Lovvorn 1987) and Chesapeake Bay (Nichols and Haramis 1980) also exhibited midwinter declines in body mass. Reductions in body mass (and fat) of Canvasbacks in North Carolina corresponded to a dietary shift from American wild celery (*Vallisneria americana*) tubers to clams (*Macoma* spp.; Lovvorn 1987). In contrast, high relative body mass of Canvasbacks wintering in Louisiana resulted from their having access to abundant, energy-rich plant foods throughout winter (Hohman 1993).

Overwinter survival probabilities of some waterfowl are influenced by their relative body mass (Haramis et al. 1986, Hepp et al. 1986; but see Krementz et al. 1989). Large energy reserves (correlate of body mass) enhance survival when birds experience food shortages and increased thermoregulatory costs. Further, energy and nutrient reserves maintained in late winter may be used to offset costs (i.e., courtship, migration, prebasic molt [females only], and energy and nutrient storage for reproduction) incurred by diving ducks in spring (Hohman et al. 1988, Hohman 1993).

If it is advantageous for diving ducks to maintain high levels of endogenous reserves during winter, then why do some birds winter at northern latitudes where, because of greater maintenance energy costs and reduced feeding opportunities, they are lighter than birds at more southerly sites? Most diving ducks wintering in northern portions of their winter ranges are males (Nichols and Haramis 1980, Alexander 1983, Haramis et al. 1985, Woolington 1993). Factors responsible for sexual differences in winter distributions of diving ducks thereby contribute to observed geographic variation in body mass. Speculation offered by Nichols and Haramis (1980) and Alexander (1983) that females are subordinate to males and competitively excluded from northern wintering areas is not supported by this study nor by studies of wintering or migrating Canvasbacks (Lovvorn 1989, Hohman and Rave 1990, Hohman 1993). Dominance relations are temporally and spatially dynamic (e.g., Lovvorn 1989). Although structurally smaller, female ducks are sometimes dominant to males (e.g., Canvasbacks, Lovvorn 1989; Blue-winged Teal, Thompson and Baldassarre 1990).

We speculate that geographic differences in mass and composition changes are related ultimately to waterfowl mating systems. Waterfowl form pair-bonds well in advance of breeding, but there is considerable

variation among taxa (Rohwer and Anderson 1988). In general, dabbling ducks (*Anas* spp.) pair in fall and winter, whereas diving ducks form pair-bonds in late-winter or spring (Weller 1965). Delays in pair formation by diving ducks have been attributed to advantages of remaining in flocks (antipredator tactic) and dispersion of foods that commonly preclude site defense (Lovvorn 1989). Regardless of its causes, a major implication of delayed pair formation in diving ducks is that males and females are able to exploit winter habitats independently.

Costs and benefits to diving ducks occupying various portions of their winter range probably differ between sexes. Wintering at northern sites may be favored in males because they are more numerous than females (Bellrose et al. 1961) and must compete for mates. If proximity to spring-staging and breeding areas (i.e., sites where birds initiate courtship and pair-bond formation) influences time of arrival and pairing success, then males wintering in the north may gain a competitive advantage over those wintering to the south (Nichols and Haramis 1980). Because of their lower body mass, survival rates of birds wintering at more northerly sites may be reduced relative to those at southern latitudes; however, the abundance of males relative to females would seem to suggest that survival risks to males wintering at northern latitudes are minimal.

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Appendix I

General Linear Models Used to Describe Differences in Size, Body Mass, and Fat (g) of Ring-necked Ducks Collected in Florida, Winter 1979–1980

		Size[a]				Body mass			Fat[b]		
Source	df	Sum of squares[c]	*F*-value	$P > F$	df	Sum of squares	*F*-value	$P > F$	Sum of squares	*F*-value	$P > F$
Model[d]	7	293.09	29.32	<0.001	8	656,254.8	48.59	<0.001	156,272.4	23.89	<0.001
Error	169	241.33			168	283,647.2			137,357.3		
Corrected total	176	534.43			176	939,902.0			293,629.7		
Size					1	75,914.4	44.96	<0.001	1407.7	1.72	0.191
Date	1	1.69	1.19	0.277	1	267,488.3	158.43	<0.001	135,268.4	165.45	<0.001
Sex	1	13.35	9.35	0.003	1	5.1	0.00	0.956	1652.2	2.02	0.157
Date*sex	1	0.66	0.47	0.495	1	124.0	0.07	0.787	2126.6	2.60	0.109
Age	1	8.95	6.27	0.013	1	8371.5	4.96	0.027	966.6	1.18	0.278
Date*age	1	4.61	3.23	0.074	1	3887.5	2.30	0.131	692.9	0.85	0.359
Sex*age	1	5.06	3.54	0.062	1	2469.1	1.46	0.228	1996.5	2.44	0.120
Date*sex*age	1	4.61	3.23	0.074	1	4878.5	2.89	0.091	2037.5	2.49	0.116

[a] Size = scores along the first principal component: a linear combination of five structural measurements based on their correlation matrix.
[b] Fat = sum of sheared skin and omental fat mass.
[c] Type III Sums of Squares (SAS Inst., Inc. 1987).
[d] Explained variance for full models: size, $r^2 = 0.55$; body mass, $r^2 = 0.70$; and fat, $r^2 = 0.53$.

Appendix II

General Linear Models Used to Describe Differences in Protein and Leg Mass (g) of Ring-necked Ducks Collected in Florida, Winter 1979–1980

		Protein[a]			Leg mass		
Source	df	Sum of squares	*F*-value	$P > F$	Sum of squares	*F*-value	$P > F$
Model[b]	8	115,611.0	36.83	<0.001	403.55	13.49	<0.001
Error	168	65,919.4			628.01		
Corrected total	176	181,530.5			1031.56		
Size	1	27,779.7	70.80	<0.001	143.82	38.47	<0.001
Date	1	7623.0	19.43	<0.001	56.35	15.08	<0.001
Sex	1	3380.9	8.62	0.004	9.78	2.62	0.108
Date*sex	1	4394.8	11.20	0.001	4.67	1.25	0.265
Age	1	2191.1	5.58	0.019	28.89	7.73	0.006
Date*age	1	846.7	2.16	0.144	20.89	5.59	0.019
Sex*age	1	965.3	2.46	0.119	4.87	1.30	0.255
Date*sex*age	1	1115.5	2.84	0.094	5.08	1.36	0.245

[a] Protein = eviscerated carcass mass.
[b] Explained variance: protein, $r^2 = 0.64$; leg muscle mass, $r^2 = 0.39$.

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BLACK-NECKED STILT FORAGING SITE SELECTION AND BEHAVIOR IN PUERTO RICO

SEAN A. CULLEN[1]

ABSTRACT.—Black-necked Stilts (*Himantopus mexicanus*) in Fraternidad Lagoon, Puerto Rico, foraged in a section of the lagoon that had consistently "deep" water (>9 cm) and the greatest abundance of prey. As wind speed increased, the foraging stilts changed their behavior from a pecking to a sweeping tactic due to the reduced visibility in the water column. *Received 26 April 1993, accepted 12 Aug. 1993.*

Most studies on the foraging ecology of shorebirds (Order Charadriiformes) have focused on coastal and estuarine systems where tides control the availability of habitat on a daily basis (e.g., papers in Pitelka 1979). Significant associations between the abundance of shorebirds and the density of their main prey have been found (Bryant 1979). However, few studies have focused on habitat use by shorebirds in a tropical or subtropical wintering ground (Robert et al. 1989).

Foraging activity may be affected by environmental factors which influence the birds' behavior or prey availability (Puttick 1984). Tide, rain, substrate permeability, and temperature can affect the foraging behavior of shorebirds (Evans 1979, Goss-Custard 1970, Myers et al. 1980, Pienkowski 1983). Increased wave action caused by wind can reduce availability of prey in shallow water (Evans 1979).

Little is known about the foraging behavior and ecology of Black-necked Stilts (*Himantopus mexicanus*) (Tinarelli 1987, Hamilton 1975). This study explores the relationship between macroinvertebrates and water level to the foraging distribution of the Black-necked Stilt and how wind speed affects stilt foraging behavior in relation to prey availability.

METHODS

Fraternidad Lagoon (12°30′N, 57°3′W), in the southwest corner of Puerto Rico, is a man-made salt works system which is subdivided into five main areas: Mangrove Pool, "A", "B", "Box", and "C" (Fig. 1). There is an increasing salinity gradient from "Mangrove Pool" to "A" to "B" to "Box" to "C".

Censuses of Black-necked Stilts in each section were made at least twice a week between 25 September and 14 November 1991. Four people censused the system simultaneously. Transects were established for macroinvertebrate sampling in "Mangrove Pool", "A", "B", and "Box" (Fig. 1). Invertebrate samples were collected eight times at approximately six-day intervals. A sweep net (30 cm × 18 cm, 17 cm deep, 0.5 mm mesh) was used for

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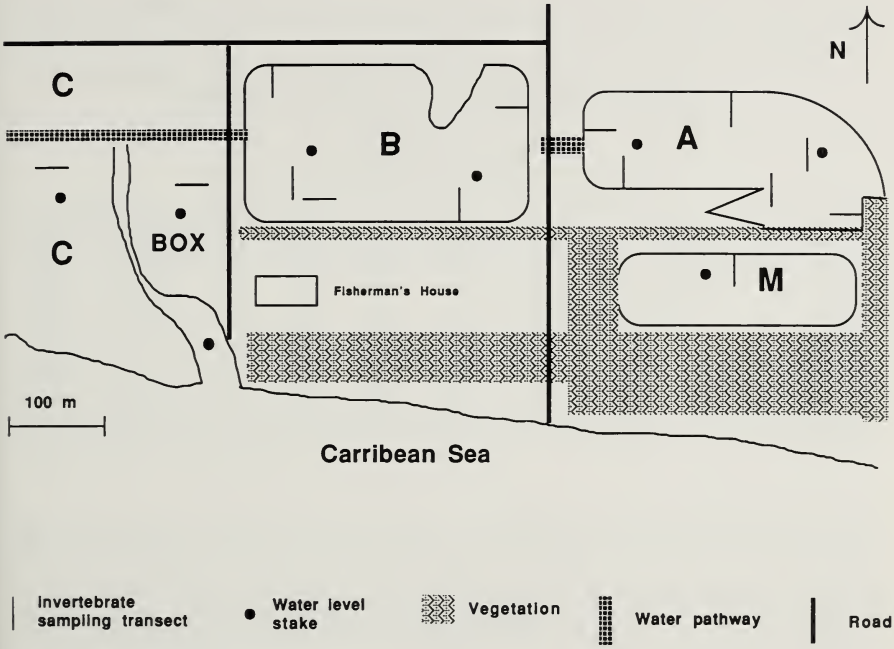

FIG. 1. Map of Fraternidad Lagoon study site.

sampling invertebrates in the water column. The sweep distance was seven steps (approx. 5 m), performed by the same person throughout the study. Along each transect two samples were taken perpendicular to the transect at locations where the water was 6 and 12 cm deep. If the water depth did not reach these levels, the samples were taken as close as possible.

To quantify invertebrate samples, I averaged the estimates made by three persons after washing the sample of the sweep net onto a 0.5 mm screen (35 cm × 31 cm). A size distribution ratio was determined from at least 15% of the sample. Three size categories were used: small (<2.5 mm), medium (2.5–3.5 mm), and large (>3.5 mm). The ratio of large, medium, and small invertebrates was applied to the total for each sweep. All sweeps collected in greater than 9 cm of water were characterized as "deep" and less than 7 cm as "shallow".

Calibrated wooden stakes were placed throughout the Fraternidad System (Fig. 1). By comparing the mean daily water levels to the sweep net data, I was able to determine days when there was "deep" water along the transects.

Behavioral observations were made on foraging Black-necked Stilts. Wind speed, location, water depth, and foraging technique were recorded for each individual. The water depth was divided into five categories according to leg length. Foraging in: 1—no water (0 cm), 2—water at mid-tarsus (5.3 cm), 3—water at tarsometatarsus (10.6 cm), 4—water at mid-tibia (14.2 cm), 5—water at belly (18.3 cm). These water depths were assigned using the mean of leg length measurements of Helmers (1991). Two types of foraging techniques were observed at Fraternidad: pecking and single scythe (Hamilton 1975).

A relationship between wind speed and the percentage of a flock sweeping for each water depth was tested with regression. Analysis of covariance was used to examine the relation-

TABLE 1

ABUNDANCE OF SIZE CATEGORIES OF WATERBOATMEN IN "DEEP" (>10 CM) AND "SHALLOW" (<7 CM) WATER, IN "A", "B" AND "BOX"

		Waterboatmen category							
		>3.5 mm		2.5–3.5 mm		<2.5 mm		Total	
Location	N	Median	SE[a]	Median	SE[a]	Median	SE[a]	Median	SE[a]
A deep	45	291.3	68.7	54.6	23.8	39.1	18.9	432.0	84.5
A shallow	31	15.1	65.2	100.1	94.6	216.7	60.2	370.0	209.4
B deep	11	334.6	180.3	30.0	50.9	50.0	73.7	565.0	197.2
B shallow	36	3.0	63.9	2.0	34.3	36.1	37.9	47.5	159.6
Box deep	5	37.3	62.2	10.8	15.2	21.0	10.9	85.5	80.0
Box shallow	4	2.0	209.2	4.0	9.5	11.0	4.9	18.0	216.7

[a] Standard error.

ship between wind speed, water depth, and the percentage of a flock sweeping, where percent sweeping was the dependent variable, water depth was the classification variable, and wind speed was the continuous variable and covariate of the model. Due to small sample size, I was unable to analyze foraging techniques of Black-necked Stilts foraging in water less than 5.4 cm (N = 6). Birds foraging in water deeper than 14.0 cm were grouped together (N = 48). All observations of foraging birds were in "A" except for three in "B".

RESULTS

Black-necked Stilts were observed foraging in eight of the 21 censuses. The mean number of birds using "A" was significantly greater than the number using "B" (Wilcoxon, $Z = 2.547$, $P = 0.0109$, N = 8). Over 99% of the Black-necked Stilts observed foraging were in water deeper than 10 cm. A total of 159 sweep net samples were collected throughout the system. Waterboatmen (Order Hemiptera, Family Corixidae) were the only animals caught. Sampling was possible in "C" only once (five waterboatmen captured) since the low water made sampling inappropriate for the rest of the study period. Eight sweeps in "Mangrove" resulted in only 11 waterboatmen (Table 1). There was a significant difference in the number of large waterboatmen among "A deep", "A shallow", "B deep", and "B shallow" categories (Kruskal-Wallis, $H = 52.029$, $P = 0.0001$, df = 3). "A deep" and "B deep" had significantly more large waterboatmen than "A shallow" and "B shallow" (Table 2). Total number of waterboatmen differed significantly among "A deep", "A shallow", "B deep", and "B shallow" (Kruskal-Wallis, $H = 52.029$, $P = 0.0001$, df = 3). "A deep" and "A shallow" had significantly more waterboatmen than "B shallow" (Table 2). In "B" west, "deep" water was available 58% of the days (N = 36). In "B" east, 36% of the days

TABLE 2

RESULTS OF MANN-WHITNEY U TESTS COMPARING THE ABUNDANCE OF WATERBOATMEN IN "A DEEP", "A SHALLOW", "B DEEP", AND "B SHALLOW"[a]

	Waterboatmen category							
	>3.5 mm		2.5–3.5 mm		<2.5 mm		Total	
Locations compared	*Z*	*P*	*Z*	*P*	*Z*	*P*	*Z*	*P*
A deep vs A shallow	4.79	.0005	1.75	.0793	4.26	.0006	1.00	.317
A deep vs B deep	0.19	.8447	0.11	.9097	0.68	.4961	0.27	.7849
A deep vs B shallow	6.19	.0006	4.71	.0006	0.47	.638	5.34	.0006
A shallow vs B deep	2.93	.012	0.88	.375	2.96	.0124	0.69	.4865
A shallow vs B shallow	2.87	.008	3.28	.003	3.97	.0005	4.08	.0005
B deep vs B shallow	3.87	.0004	3.31	.0045	0.36	.7154	2.94	.0132

[a] The total number (all size categories combined) of Waterboatmen is also compared between pools. Sequential Bonferroni corrected for table-wide significance (Rice 1989).

(N = 39) had "deep" water. "Deep" water was available every day in "A" (N = 40).

As wind speed increased, the arcsine-transformed percentage of flock members sweeping increased when foraging at a mean water depth of 10.6 cm (Model 1 regression, $r^2 = 0.453$, $P = 0.0001$, N = 48) and at a

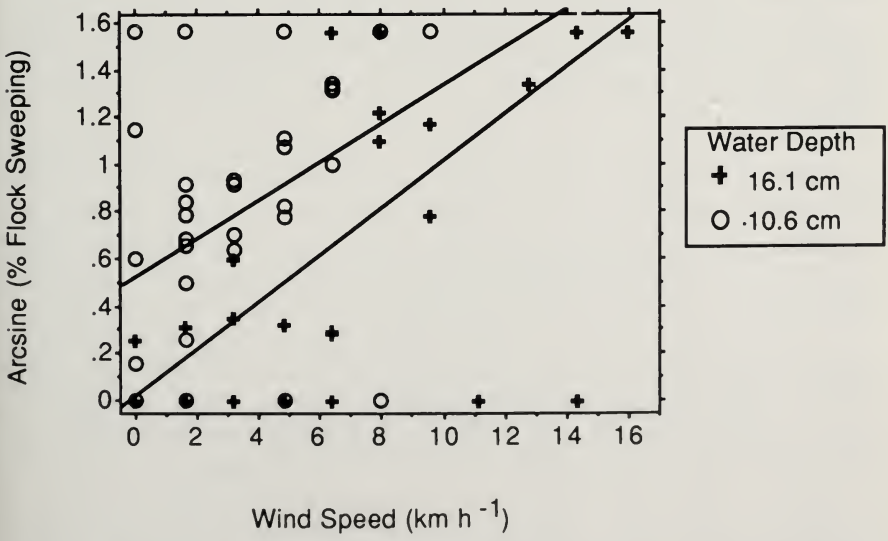

FIG. 2. Regression plot of the arcsine-transformed percentages of stilt flocks sweeping in relation to the wind speed while foraging at mean water depths of 16.1 cm (N = 37) and 10.6 cm (N = 48).

mean water depth of 16.1 cm (Model 1 regression, $r^2 = 0.14$, $P = 0.0227$, N = 37) (Fig. 2).

DISCUSSION

Waterboatmen, the only invertebrate found in 159 sweeps of the water column, feed on algae and other organic matter (Essig 1942). Black-necked Stilts peck at waterboatmen which come to the surface for air. Visually foraging Black-necked Stilt may focus on areas with the greatest abundance of larger waterboatmen to maximize food intake per catch and perhaps because larger waterboatmen are easier to see.

In sweeping, Black-necked Stilts rely on tactile cues to capture prey (Hamilton 1975). Sweeping Black-necked Stilts could optimize capture of food by foraging in areas with greatest prey abundance and larger prey size (Baker and Baker 1973).

Black-necked Stilts foraged primarily in "A deep" and only rarely elsewhere. They highly favored water deeper than 10 cm. "A deep" is the preferred habitat for stilts in Fraternidad Lagoon. All of the sections beside "A" and "B" had low numbers of prey and were not used as foraging sites (Table 1). "A deep" and "B deep" had a greater average number of large (>3.5 cm) waterboatmen than "A shallow" and "B shallow". "A deep", "B deep", and "A shallow" had the greatest prey abundance. Even though "A shallow" had similar abundance of prey as "A deep" and "B deep", the prey were smaller. Black-necked Stilts appear to prefer the larger prey and greater prey abundance found in deep water. However, stilts foraged in "A deep" significantly more than in "B deep".

Deep water (>9 cm) was available every day in "A" but only 36% and 50% of the days in "B" west end and east end, respectively. Black-necked Stilts would have found deep water in "A" at all times (i.e., abundant large waterboatmen) whereas "B" would typically have shallow water (i.e., few waterboatmen of any size). By foraging in "A deep", stilts were in a location that favored both visual and tactile techniques.

As wind speed increases, a Black-necked Stilt is more likely to sweep instead of peck (Fig. 2). Wind causes waves on the surface of the water. Waves reflect and diffract the sunlight and reduce vision through the water column, making it difficult to locate waterboatmen coming for air (pers. obs.), and causing stilts to switch to tactile feeding.

Attempts were made to determine success rates of pecking and sweeping Black-necked Stilts. Although success rates supposedly can be determined for Black-necked Stilts by counting a jerky swallowing motion following a peck as a success (Tinarelli 1987), I observed birds which had obviously captured a waterboatman but which did not perform jerking

behavior. Their ability to store prey in their bill and/or swallow without a jerking motion made comparisons of the two techniques inappropriate.

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WINTER SURVIVAL RATES OF A SOUTHERN POPULATION OF BLACK-CAPPED CHICKADEES

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ABSTRACT.—Using the Jolly-Seber method of capture and reobservation, we estimated monthly winter (1989–1990, 1990–1991) survival rates of 321 color-marked Black-capped Chickadees (*Parus atricapillus*) and compared survival rates among three habitat types in central Pennsylvania: suburban habitat, forest habitat with supplemental food, and forest habitat without supplemental food. Chickadee survival rates differed ($P = 0.018$) among habitats. Monthly winter survival rates ($\bar{x} \pm$ SE) for chickadees in the forest habitat without supplemental food (0.81 ± 0.05) differed from both the forest habitat with supplemental food (0.93 ± 0.02) and the suburban habitat with supplemental food (0.94 ± 0.02). Survival rates of chickadees did not differ ($P > 0.25$) between the two habitat types where supplemental food was available. The difference in survival rates between chickadees with and without access to supplemental food was greatest in October and March, months when dispersal of chickadees may occur, suggesting that feeders were influencing movements of chickadees (survival on the study site) rather than actual survival. *Received 24 June 1993, accepted 1 Feb. 1994.*

The range of the Black-capped Chickadee (*Parus atricapillus*) extends from Alaska, across Canada, and into the northern United States (Smith 1991). Pennsylvania is on the southern edge of the Black-capped Chickadee's range. In rural northern areas with seasonally severe temperatures, survival rates of Black-capped Chickadees with access to supplemental food are higher than survival rates of chickadees without access to bird feeders (Brittingham and Temple 1988, Desrochers et al. 1988). However, the effect of supplemental feeding on survival rates of chickadees at the southern edge of their range, where winter temperatures are much milder, is unknown.

In addition to occupying a wide geographic range, Black-capped Chickadees are found in a wide range of habitats and are common in both forest and suburban areas during the winter. Suburban habitats differ from forest habitats in a number of ways, some of which may be beneficial to wintering chickadees. For example, bird feeders are abundant in most suburban areas. Other factors of suburbanization that may benefit chickadees include access to water during winter, decreased abundance of native predators, increased day length from artificial lights, and increased temperatures (Erz 1966). On the other hand, some changes associated with suburbanization, such as an increase in cats, dogs, and rats near human dwellings (Wilcove 1985), could result in a decrease in survival rates of birds. In addition, birds in suburbia are exposed to a variety of

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anthropogenic hazards, including cars and windows (Banks 1979, Hickey and Brittingham 1991, Klem 1991).

We compared winter survival rates of Black-capped Chickadees among three habitat types (suburban, forest without feeders, and forest with feeders) to determine whether survival rates differed among the surburban and the two forest habitats and to isolate the influence of supplemental feeding on survival rates from other aspects of suburbanization that may influence winter survival rates. We tested whether chickadees with access to feeders (suburban and forest with feeders) had higher survival rates than chickadees without access to supplemental food (forest without feeders) and whether the magnitude of the effect of supplemental food varied with temperature.

STUDY SITES AND METHODS

Study sites.—We established study sites within three habitat types (suburban, forest without feeders, and forest with feeders) and attempted to maintain approximately the same number of marked Black-capped Chickadees in each habitat type. We banded chickadees at one forest site with feeders, at three suburban sites, and at three forest sites where feeders were not available. Multiple banding sites were necessary for the latter two habitat types because chickadees in those areas were more difficult to capture.

The suburban sites were located in College Heights, Park Forest, and Woody Crest neighborhoods, State College, Centre County, Pennsylvania. These sites were approximately 1.2 km from each other. All suburban sites had mature trees and bird feeders located throughout. Average age of the homes in each neighborhood ranged from 26 to 70 years.

The three forest sites without feeders were located in Rothrock State Forest, Huntingdon County, Pennsylvania. The area was a mature forest dominated by oak (*Quercus* spp.), maple (*Acer* spp.), and pine (*Pinus* spp.), with small sapling and pole stands, gullies, steep talus slopes, and intermittent streams intermixed throughout the area. Two of the forest sites were approximately 2 km apart, and the third site was approximately 4 km from the other two sites. All sites were at least 1.6 km from residential areas, which might have been a source of supplemental food or domestic predators. The forest site with feeders was located at Shaver's Creek Nature Center within Rothrock State Forest, Huntingdon County, Pennsylvania. The feeders were filled year-round with black-oil sunflower seeds. Suet feeders also were present during the winter months. The nature center was approximately 4 km from the other forest sites.

Suburban survey.—Thirty residents were randomly selected from each neighborhood and asked to participate in the survey. Twenty-four residents from the three neighborhoods were willing to participate. Residents were asked five questions—(1) What is the size of your lot? (2) Do you have a bird feeder? If yes, during what seasons do you keep the feeder filled? What type of bird seed is placed in the feeder? (3) Do you have a bird bath? (4) Do you have a bird house? (5) Do you own a pet? If yes, what type of pet? and to your knowledge has the pet ever captured any birds?

Capture and marking.—At each site, we captured Black-capped Chickadees using mist nets. On the suburban sites, we also used feeder traps with a manual release. We began to capture Black-capped Chickadees in September in both 1989 and 1990 and continued capturing birds until the following March of each year. The majority of the banding occurred in October and November except at the Shaver's Creek Nature Center site during the second

year when we banded primarily in early January. We banded each Black-capped Chickadee with a USFWS aluminum leg band and three colored leg bands. Each individual had a unique combination of colored bands so birds could be visually identified in the field. From September through December, birds were aged from shape and wear of the rectrices and recorded as juveniles or adults (Meigs et al. 1983). When we were unsure, individuals were recorded as unknown. After December, the ages of newly captured birds were also recorded as unknown. All banded birds that were still alive the following fall were classified as adults. We did not determine the sex of banded chickadees.

Monthly survival rates.—From October–May, we attempted to relocate visually each Black-capped Chickadee every month. Observations were made throughout the day, and we regularly searched areas adjacent to our sites for birds which may have moved short distances. Monthly survival rates ($\bar{x} \pm$ SE) of chickadees at each study site were calculated by the Jolly-Seber method that uses capture and reobservation data (Jolly 1965, Seber 1965, Clobert et al. 1987). We did not calculate monthly estimates for months when fewer than five individuals were captured or reobserved. These data gaps occurred primarily early in the winter when we had few marked individuals. We used one-way and two-way analysis of variance and a Tukey's test ($\alpha = 0.05$) to test for differences in average monthly survival rates among different groups of chickadees (Brittingham and Temple 1988).

Survival rates and temperature.—We obtained data on ambient temperatures from the National Oceanic and Atmospheric Administration (NOAA) weather station in State College, Pennsylvania. We did not obtain separate temperature data for the forest sites, but presumably these sites would be a few degrees colder on average than the suburban sites (Erz 1966).

In northern areas, winter survival rates of chickadees are dependent to some extent on the interaction between winter severity and winter food supply (Brittingham and Temple 1988, Smith 1991). To determine if winter survival rates differed with ambient temperatures and food supply at the southern edge of the chickadee's range, we examined the effects of temperature on survival rates of chickadees with and without supplemental food in a number of ways. First, using analysis-of-covariance, we tested whether mean monthly survival rates of chickadees with and without supplemental food varied linearly with mean monthly temperature.

Fat deposition in chickadees and other small birds is maintained at a level that allows an individual to survive overnight under expected or average weather conditions (Evans 1969). As a result, monthly survival rates may be less dependent on the actual value of the mean temperature and more dependent on how close the mean temperatures are to the normal or "expected" temperatures. For each month, we used the 30-year (1951–1980) mean temperature as the expected temperature. We separated the months of our study into two groups, months when the mean temperature was at or above average and months when the temperature was below average, and tested whether survival rates of chickadees with and without supplemental food differed between months when the monthly temperature was above or below normal.

Brittingham and Temple (1988) reported that the positive effect of supplemental feeding on survival rates was most pronounced during extended periods of cold temperatures (>5 days below −18°C). They suggested that supplemental food was relatively unimportant during mild or average winter weather but was extremely important during extended cold spells. In Pennsylvania, the periods of cold temperatures were not as cold or as long as in Wisconsin. During the two winters of this study, the coldest mean temperature that occurred for more than four consecutive days within a month was −6.67°C. Therefore, to test whether the effect of supplemental feeding was greatest during months with extended periods of cold temperatures, we categorized the months as months when the temperature fell below

TABLE 1

CAPTURE AND OBSERVATION DATA USED TO CALCULATE SURVIVAL RATES OF CHICKADEES IN SUBURBAN AND FOREST HABITATS (1989–1991)

Study site[a]	Habitat[b] type	Number of chickadees banded	Age of[c] chickadees			Number of recaptures and observations
			Adult	Juv	Unkn	
RR1	FNF	45	29	22	1	169
RR2	FNF	31	24	9	8	132
WDF	FNF	41	17	8	28	92
SSC	FF	123	33	9	99	349
PFS	SF	34	24	14	2	141
CHS	SF	29	16	12	4	146
WCS	SF	18	4	4	10	58

[a] Study site: RR1 = Rothrock forest site 1; RR2 = Rothrock forest site 2; WDF = Whipple Dam forest site; SSC = Shaver's Creek forest with supplemental food; PFS = Park Forest suburban site; CHS = College Heights suburban site; WCS = Woody Crest suburban site.

[b] Habitat type: FNF = forest habitat, no feeders; FF = forest habitat with feeders; SF = suburban habitat with feeders.

[c] Number of chickadees does not equal number of banded chickadees because chickadees banded in year 1 and still present on the site in year 2 are counted twice.

−6.67°C on four or more consecutive days and months when the temperature did not fall below −6.67°C on at least four or more consecutive days and tested whether survival rates of chickadees with and without supplemental food differed between the two groups of months.

RESULTS

Study site survey.—Average size (±SE) of the suburban area home lots was 0.24 ha ± 0.02 with dense vegetation or patches of native woodlands often adjacent to at least one side of the lot. Fifty-eight percent of those surveyed had bird feeders, 29% had bird baths, and 63% had bird houses in their yards. Seventy-five percent of those who fed birds maintained feeders year-round with a variety of foods. Thirty percent of the residents owned cats and 48% owned dogs. Respondents reported that 100% of the cats and 9% of the dogs had caught birds.

Banding data.—We banded 321 chickadees and made 1087 reobservations of these birds (Table 1). When chickadees of unknown age were excluded, we detected no difference ($\chi^2 = 4.4$, df = 2, $P > 0.1$) in the age composition of birds banded on the three types of sites. The percentage of adults was 64% on the forested sites where supplemental food was not available, 79% on the forested site where supplemental food was available, and 59% on the suburban sites. In addition, the percentage of adults in the population did not differ ($\chi^2 = 0.12$, df = 1, $P > 0.5$) between sites where supplemental food was not available and sites where supplemental food was available (64% vs 66%) (Table 1).

Survival rates and habitat type.—Average monthly survival rates (N = 28) of Black-capped Chickadees differed among habitat types (F = 4.73, df = 2, 25, P = 0.018). Average monthly survival rates (± SE) of chickadees on the forest sites where supplemental food was not available (0.81 ± 0.05, N = 10) differed significantly ($P < 0.05$) from survival rates of chickadees on both the forest site with supplemental food (0.93 ± 0.02, N = 7) and the suburban sites (0.94 ± 0.02, N = 11) where supplemental food was also available. We did not detect differences in survival rates of chickadees ($P > 0.25$) between the forest habitat with supplemental food and the suburban habitat. Because monthly survival rates did not differ between the two habitat types where supplemental food was available (suburban and forest with feeder) and both differed from the habitat type where supplemental food was not available (forest without feeders), all remaining analyses were between sites where feeders were available (suburban and forest with feeder combined) and sites where supplemental food was not available.

Monthly variation and survival rates.—Survival rates varied among months (F = 2.90, df = 5, 16, P = 0.05), with the presence of supplemental food (F = 22.58, df = 1, 16, $P < 0.0001$), and with the interaction among months and presence of supplemental food (F = 3.14, df = 5, 16, P = 0.04) (Fig. 1). In all months, survival rates of chickadees with access to supplemental food was higher than survival rates of chickadees without access to supplemental food, but the difference was most pronounced in October and March. During those months, survival rates of individuals without access to supplemental food fell to approximately 0.60, but survival rates of birds with access to supplemental food remained >0.90.

Survival rates and temperature.—During the months of our study, the mean ($\bar{x}$ ± SE) monthly temperature was 4.1°C ± 5.6 and the mean monthly minimum temperature was −0.94°C ± 4.9. During one month, the temperature fell below −13°C on 14 days and below −21°C on one day. During a second month, the temperature fell below −10°C on 4 days and below −15°C on one day. The mean monthly temperature was at or above average during nine months and was below average during two months. Mean temperatures for each month did not exceed or fall below normal (1951–1980) by more than 2.8°C except December 1989 which was 6.8°C below normal. During the two winters of this study, temperatures fell below −6.67°C on four or more consecutive days during four months.

We did not detect a difference in survival rates with mean monthly temperature (F = 1.75, df = 1, 25, P = 0.20) or between months when the mean temperature was below normal and months when it was above normal (F = 3.25, df = 1, 25, P = 0.08). In addition, we did not detect

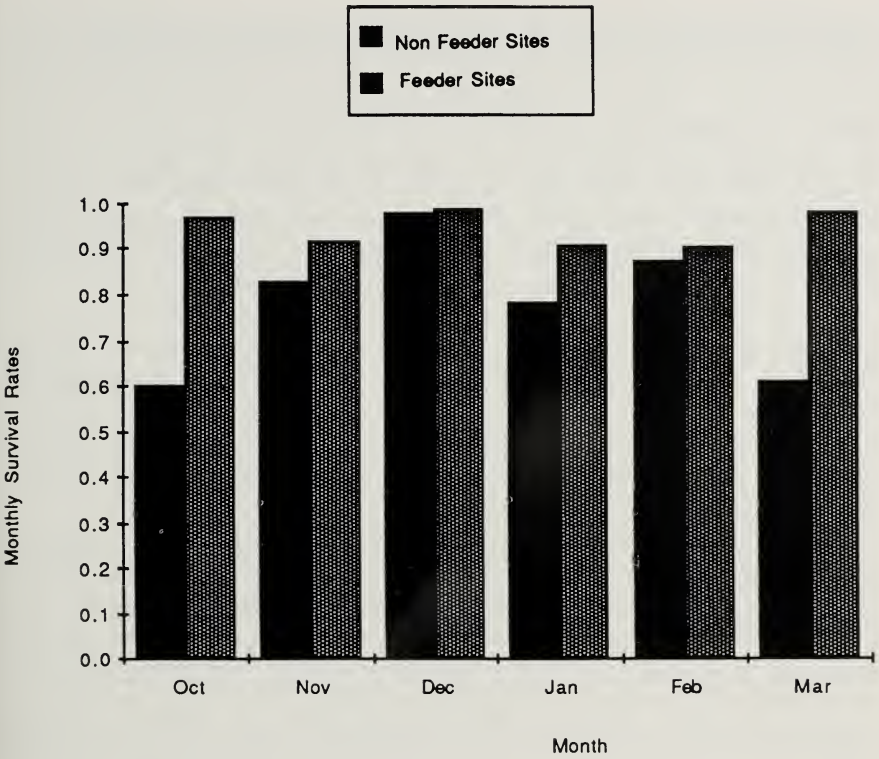

FIG. 1. Mean monthly survival rates of chickadees with and without access to bird feeders in Centre and Huntingdon counties, Pennsylvania, during the winter (1989–1991).

a difference in survival rates between cold months (≥4 consecutive days below −6.67°C) and moderate weather months (≤4 consecutive days above −6.67°C) ($F = 1.20$, df = 1, 25, $P = 0.28$).

DISCUSSION

Numerous studies have shown that Black-capped Chickadees and European tits (*Parus* spp.) with a source of supplemental food have higher survival rates than individuals without access to supplemental food (Jansson et al. 1981, Brittingham and Temple 1988, Desrochers et al. 1988, Orell 1989). Bird feeders were common throughout the suburban sites, and all the chickadees banded on those sites used the feeders. Therefore, we attributed the positive effect of suburbanization on survival rates to the numerous bird feeders present in the suburban habitat.

Wilcove (1985) speculated that effects of suburbanization, such as in-

creased abundance of domestic predators and higher disturbance levels, may negatively affect survival rates, but we did not detect any differences in the survival rates of chickadees in the suburban habitat and the forest habitat with supplemental food. Perhaps an increase in numbers of domestic predators in suburban areas was offset by a decrease in native predators. On the other hand, chickadees with access to feeders may not have to expend as much time searching for food, thus, decreasing their time exposed to predators (Powell 1974, Jansson et al. 1981), or they may be less vulnerable to domestic predators than other bird species.

The survival rates we estimated for our chickadee populations describe continued presence on the study site. The complement of these rates include both mortality and emigration. We had no way of distinguishing between the two types of losses because birds were never found dead. However, the timing of disappearance and the environmental circumstances occurring at the time of disappearance provide evidence to separate the two types of losses.

The greatest difference between survival rates of chickadees with and without supplemental food occurred in October and March. Concentrated movements of chickadees occur in the fall and spring (Smith 1991). Chickadee movements in the fall (e.g., juvenile dispersal) have usually stabilized by late October (Weise and Meyer 1979, Desrochers and Hannon 1989). In the spring, chickadee movements may begin as early as mid-March when individuals of low dominance status begin to wander (Smith 1991). The timing of loss in our study suggests that individuals which disappeared may have emigrated instead of died. The environmental conditions in October and March support this hypothesis. October is generally a mild month and natural food supplies are still abundant. March can be a time of food shortage, but at least during this study, March temperatures were above or near normal. Consequently, we suspect supplemental feeding in Pennsylvania had an effect on movement instead of on actual survival. Supplemental feeding may have caused chickadees to settle earlier in the fall and move out later in the spring.

Our results differ from those reported in Wisconsin where survival rates of chickadees were affected by temperature and the benefits of feeders were most pronounced during extended periods of cold temperatures (Brittingham and Temple 1988). In addition, the authors provided strong evidence that bird feeders influenced actual survival rates instead of movement (Brittingham and Temple 1988). We did not find any relationship between cold temperatures and winter survival rates of Black-capped Chickadees in Pennsylvania. The two winters during this study were normal winters for central Pennsylvania, thus the chickadees may have had sufficient reserves for those temperatures. During an unusually cold win-

ter, we might see a relationship between survival rates, supplemental food, and temperatures.

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NESTING BEHAVIOR OF A RAGGIANA BIRD OF PARADISE

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ABSTRACT.—We made observations of a nest of a Raggiana Bird of Paradise (*Paradisaea raggiana*) for 22 days. The single nestling was attended only by the female and was fed only arthropods until day 5, and thereafter a mix of arthropods and fruit. Evidence from regurgitation of seeds at the nest indicates that the parent subsisted largely on fruit. This dietary dichotomy conforms to that of other polygynous birds of paradise and accords with socioecological predictions concerning single-parent nestling care. *Received 3 Aug. 1993, accepted 1 Feb. 1994.*

Many aspects of the life history of birds of paradise (Paradisaeidae) are at least superficially understood (Gilliard 1969, Cooper and Forshaw 1977, Diamond 1981, Beehler 1989). One notable exception is nesting biology which is inadequately documented for many paradisaeid species (Cooper and Forshaw 1977). In spite of recent contributions (Pruett-Jones and Pruett-Jones 1988; Frith and Frith 1990, 1992, 1993a, b; Mack 1992), the nests of 13 species remain undescribed, and 26 species have never been studied at the nest (Cooper and Forshaw 1977; Beehler, unpubl.). Here we provide the first detailed description of nesting behavior of the Raggiana Bird of Paradise (*Paradisaea raggiana*) in the wild, one of the best-known members of the family, and Papua New Guinea's national symbol.

The Raggiana Bird of Paradise is a common, vocal, and widespread species of forest and edge that inhabits lowlands and hills of southern, central, and southeastern Papua New Guinea (Cooper and Forshaw 1977). It is strongly sexually dimorphic. The male is larger than the female and exhibits an emerald green throat, an elongated central pair of tail wires, and dense silky orange (or in some subspecies orange-red) pectoral plumes that are erected into a cascade during vocal and kinetic courtship display. By contrast, the female (and subadult male) is colored in browns, tans, and dull yellow and typically is silent and unobtrusive. The Raggiana displays in classic lek pattern, where several males occupy canopy branches of a forest tree and display to and mate with visiting females (Frith 1981, Beehler 1988).

Subsequent to mating, females receive no assistance from males in nest building, incubation, or raising offspring (Cooper and Forshaw 1977).

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Female-only nest care appears universal among lek-breeding bird species (Bradbury 1981, Beehler 1987) and apparently places considerable demands on the parent provisioning offspring.

In the Ribbon-tailed Astrapia (*Astrapia mayeri*), the largely frugivorous female feeds her offspring a diet that includes substantial animal prey (Frith and Frith 1993a). Dharmakumarsinhji (1943) reported that a captive Raggiana female fed her nestling orthopterans. Other zoo-bred *Paradisaea* species were fed arthropods and fruit (Muller 1974, Todd and Berry 1980, Searle 1980). It has been predicted that in the wild, Raggiana females might feed their nestling a diet mostly of arthropods (Beehler 1987) in order to satisfy the offspring's demands for protein and lipid (Snow and Snow 1979).

STUDY AREA AND METHODS

We made observations at Varirata National Park, 20 km E of Port Moresby, Central Province, Papua New Guinea, 9°30′S, 147°20′E, 840 m asl, in July and August 1990. On 20 July 1990, BMB flushed a presumed female Raggiana. The following day, after flushing the bird again, BMB discovered its nest, hidden in climbing bamboo, 7.5 m up in a small tree (*Rhus taitensis*: Anacardiaceae). Observations began on 27 July and continued until 17 August when the nestling died. The nest was observed for 170 h during the 22 days, approximately 60 h before the nestling hatched (5 August, ca 10:45 h) and 110 h during the 12 days that it lived. Activity at the nest was observed from a blind on the ground, constructed of saplings and black plastic, 22 m from the nest tree, using a spotting scope with 20× eyepiece. The nest was observed during 22 days. Observation periods began ca 07:00 h and usually continued until 16:00, in some cases with interruptions. All nesting behaviors were recorded, including (1) presence or absence of the parent; (2) arrival and departure times; (3) pattern of nest arrival; (4) time spent feeding the chick; (5) chick maintenance; and (6) numbers and kinds of food delivered to the chick.

The duration and timing of parental activity, such as egg turning and nestling attendance, were timed when possible. Observations, in which head or bill movements and regurgitations were counted, were also made. The dead nestling was preserved in an ethanol:formalin solution and necropsied at the Dept. of Pathology, National Zoological Park, Washington, D.C.

RESULTS

During the nine days preceding egg hatching, the female incubated for ca 75% of the time (Fig. 1). On 2 August it rained heavily, and the bird incubated for >90% of the observation period, not leaving the nest until the rain stopped. After the nestling hatched, the proportion of time the parent was present steadily decreased to an average of 33% of the time over the last four days. Absences from the nest did not exceed 45 minutes until 11 August when the female made a series of afternoon absences, followed by little or no brooding, and was once absent for more than an hour. The nestling was a few hours over six days old at that point. This

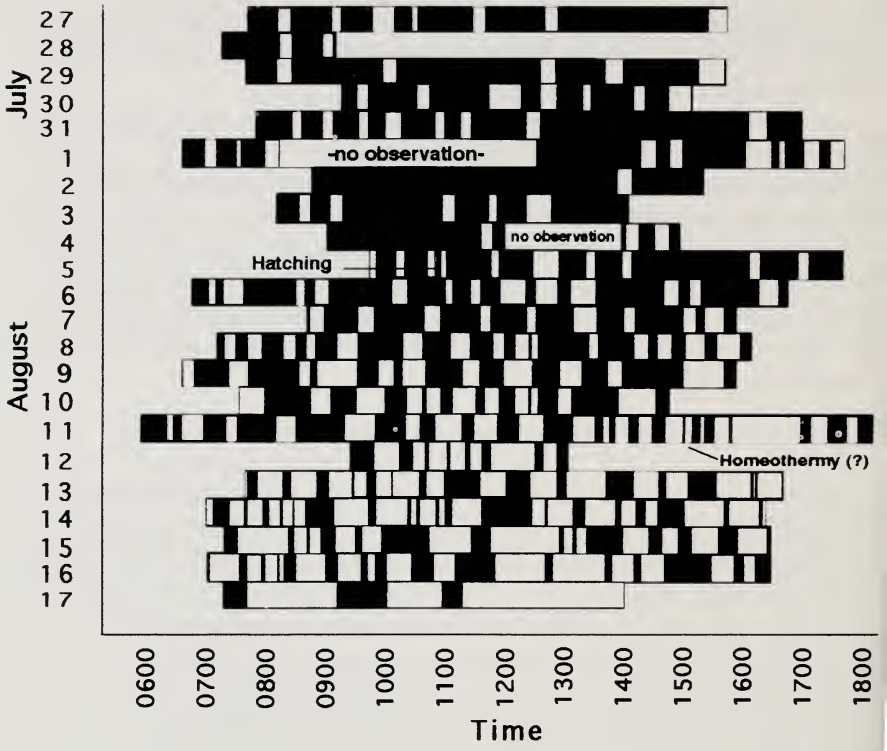

FIG. 1. Time budget for nesting female Raggiana Bird of Paradise. Black represents time female is at nest, white away from nest.

change in behavior by the female may have coincided with homeothermy of the nestling.

The female remained on the nest during rain, but if rain began while she was away from the nest, she did not return immediately. This was apparent on 16 August when rain began at 11:11 h, and intermittent downpours occurred throughout the afternoon. On four occasions the female failed to return when rain started, and the nestling was left unattended in the rain for a total of more than 65 min. The following day the female remained absent for protracted periods (Fig. 1) and did not follow her usual sequence of feeding and nestling maintenance. The nestling was not visible and was probably not capable of taking food due to its weakened state. The female left at 11:20 h and had not returned when observation ended at 14:05. The dead chick was cold when it and the nest were collected at 15:30 h.

The nest was a bowl-shaped structure with an exterior diameter of ca

150 mm and an interior diameter of ca 110 mm. It was made of entwined supple roots, vines and leaves, lined with an extensive mat of thin, wire-like fern stems. A live epiphytic orchid and live fern were part of the structure of the cup.

The female, with two brief exceptions, sat in the same position nearly perpendicular to our line of sight. She normally departed from the far side of the nest via a small branch. On several occasions, she left from the near side of the nest. She periodically stood in the nest with her head down, presumably rolling the egg.

The female periodically stood in the nest and attended the nestling. These bouts of nestling maintenance were accompanied by occasional nest probing. By the time the nestling died the female was in a constant half-stand or crouch, usually with her back feathers somewhat elevated.

The female was constantly alert during the incubation and nestling periods. Her head was almost constantly moving, shifting position in small jerky movements at intervals of less than a second. The only major change in this behavior occurred during rain, when the bird became more quiescent. The female also made frequent bill movements. These included quick head or bill shaking movements, opening and closing her beak rapidly from one to six times, and slowly opening her beak wide until mandibles were nearly perpendicular and then snapping them closed.

The female frequently regurgitated seeds to the base of her bill before reswallowing them or rolled seeds to her bill tip before reswallowing. The female often increased the frequency of regurgitations before leaving the nest and on 10 occasions left carrying a seed in her bill tip. The red or red-brown drupe seeds were up to 15 mm long. She drank water droplets from her back and from leaves during rain on four occasions. She spent little time (18 occasions of <2 sec) preening, probing, or picking her feathers.

The female regurgitated seeds of a variety of sizes and shapes and thus, over the 22 days of observation, may have fed herself largely or exclusively on fruit. The nestling was fed exclusively on arthropods for the first five days of its life and thereafter occasionally was fed fruit (drupes) or pulpy mash that may have been figs. The feeding visit rate remained at slightly over one per hour except for 12 and 13 August when it increased sharply (Fig. 2).

The number of regurgitations of meal components (boluses) delivered per feeding visit increased after the fourth day (Fig. 2). The higher number of feeding visits per hour on 12 and 13 August coincides with a decrease in the number of boluses per feeding, and suggests that the total delivery of food was probably not different during those two days. Our impression is that bolus size increased during the nestling period, but data

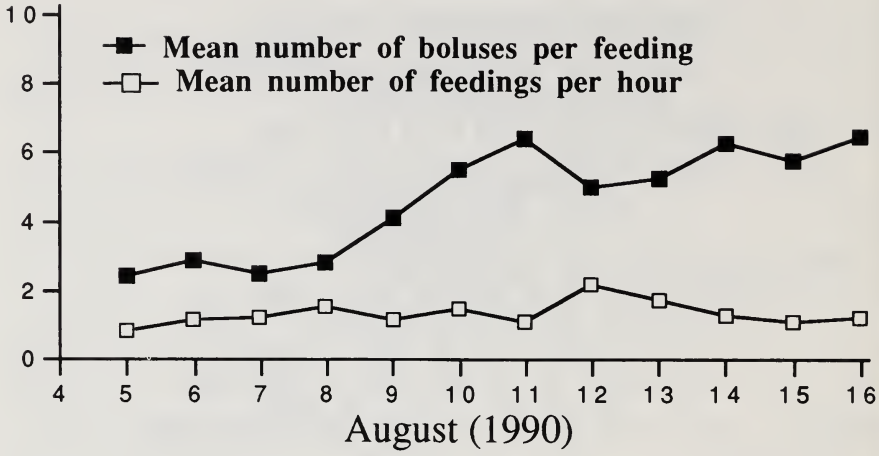

FIG. 2. Feeding frequency of nestling by female.

are inadequate to test this. Time invested in feeding the nestling did not change over the study (Fig. 3C). Time spent by the adult perched in the nest tree looking around before returning to the nest increased during the last two days (Fig. 3B). As the nestling aged, the female spent more time tending the nest and nestling (Fig. 3A). The female typically ate items picked from the nest cup immediately after feeding the nestling. She ate fecal sacs on more than a dozen occasions, never was observed carrying a fecal sac from the nest, and on three occasions took a fecal sac directly from the nestling's raised posterior. The largest fecal sac was estimated to be 25 mm (longest dimension).

The behavior of the female was cryptic. She typically looked around from the well-hidden nest for a few seconds before departing and looked around considerably longer before reentering the nest (Fig. 3B). We found no droppings under the nest tree and no regurgitated seeds or other evidence of food. The female frequently left the nest carrying seeds. She carried away the egg shell after the chick hatched.

The female sat quietly and still when predators were present. On 3 August, a Doria's Hawk (*Megatriorchis doriae*) perched 20 m from the nest tree and 31 minutes later perched 25 m from it. The female remained still throughout this period. Other potential predators, including a Brahminy Kite (*Haliastur indus*), Grey Crow (*Corvus tristis*), several Hooded Butcherbirds (*Cracticus cassicus*), and a Stout-billed Cuckoo-Shrike (*Coracina caeruleogrisea*), drew the same response as did passing mixed foraging flocks. Several small passerines perched in the nest tree, within two m of the nest, without drawing a response from the female Raggiana.

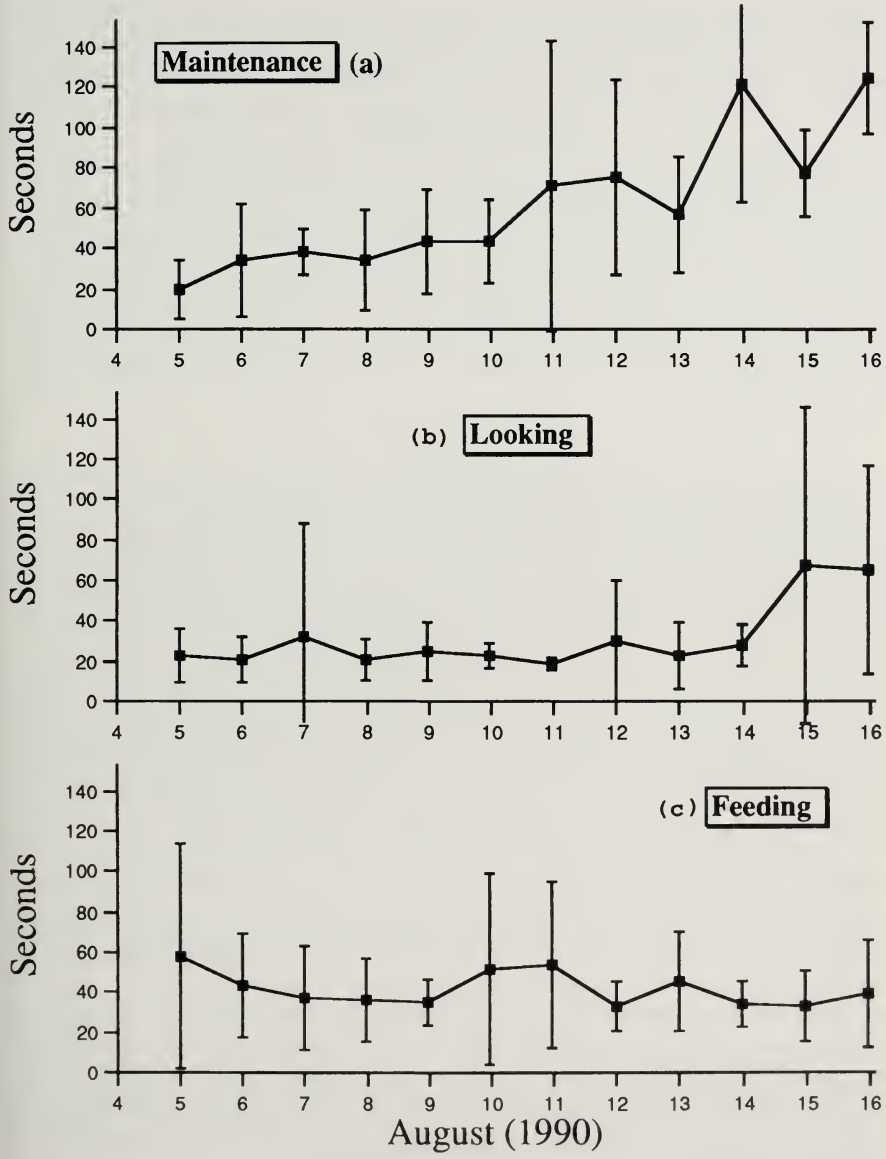

FIG. 3. Average time a female Raggiana Bird of Paradise spent in (A) nest maintenance following a nestling feeding bout, (B) looking around (typically from horizontal branch immediately below nest) before entering nest with food, and (C) feeding nestling. Bars indicate means ± SD.

The only exception occurred when several female or young male Raggianas flew near the nest tree, and the female chased one of them from the area. Birds of paradise are known to predate nest contents (Beehler, pers. obs.). The chick appeared to be silent and only made itself visible above the nest cup when the female returned from foraging.

The dead nestling had the following measurements: mass = 100 g; tarsus = 38.8 mm; posterior gape to beak tip = 23.4 mm; bill tip to pygostyle = 130 mm; wing span = 196 mm. Feathers were largely ensheathed, leaving areas of skin bare. The nestling was male, had no evidence of infectious disease, exhibited "no specific gross or histologically identifiable cause of death," and death was "perinatal, stress-related" (R. Montali, pers. comm.). It weighed 54% of mean adult female mass (LeCroy 1981).

DISCUSSION

The time budget for the incubating female (Fig. 1) is consistent with that of frugivorous birds (Snow 1962, 1976). The female was able to provision herself and spend a majority of time incubating. Some sexually dimorphic frugivorous species (e.g., Crested Bird of Paradise [*Cnemophilus macgregorii*]) feed their offspring entirely on fruit (Frith and Frith 1993b), while others (e.g., Short-tailed Paradigalla [*Paradigalla brevicauda*] and Ribbon-tailed Astrapia [*Astrapia mayeri*]) feed their young arthropods and fruit (Frith and Frith 1992, 1993a). The Raggiana fed mostly arthropods to the young bird, and the difficulty in obtaining arthropods as compared to fruit may explain the shift to about two-thirds of the time foraging (Fig. 1). This reliance on arthropods for nestling diet is consistent with observations of provisioning of nestlings by four captive bird of paradise species: King (*Cicinnurus regius*) (Bergman 1957), Superb (*Lophorina superba*) (Timmis 1968), Raggiana (Dharmakumarsinhji 1943, Searle 1980), and Magnificent (*Cicinnurus magnificus*) (Everitt 1965).

Lill (1976) and Snow (1976) suggested that provisioning young is a fundamental constraint for bird species with female-only nest attendance. In this, diet and clutch size may play significant roles. The reliance on low-protein, low-lipid, high carbohydrate fruit by manucodes *Manucodia* spp. (Paradisaeidae) has been used as an explanation for the retention of monogamy in these species (Beehler 1983, 1985).

The reliance on arthropods for nestling diet may produce a nutritional bottleneck during nesting in the Raggiana Bird of Paradise. While this high reliance requires greater foraging time, the bird continues brooding during rain. We suggest that prolonged rain places the single parent Raggiana in a demanding situation: if she forages during the rain, she risks

losing her offspring to exposure, and if she broods, she risks weakening or starving her young. At Varirata, the Raggiana Bird of Paradise nests in the middle of the dry season, when risk of prolonged rains is minimal.

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DIET OF PIPING PLOVERS ON THE MAGDALEN ISLANDS, QUEBEC

François Shaffer and Pierre Laporte

Abstract.—Piping Plover (*Charadrius melodus*) droppings were sampled at four sites on Magdalen Islands beaches, Quebec, in order to assess diet during the breeding season. Fragments of organisms found in feces were used to identify the various prey consumed. Staphylinidae (43.8%), Curculionidae (31.5%), and Diptera (31.5%) were the most commonly found invertebrates in the feces. The Piping Plover's consumption of different prey items appears to reflect their availability in the habitat. *Received 10 Aug. 1993, accepted 15 Dec. 1993.*

The Piping Plover (*Charadrius melodus*) has been on the list of endangered species in Canada since 1985 (Haig 1985). In the United States, it is considered endangered in the Great Lakes area and threatened elsewhere (U.S. Fish and Wildlife Service 1985). Previous studies of the Piping Plover have focused on its population, biology, and habitat quality, but knowledge of the Piping Plover's diet remains scanty. The Piping Plover's precarious status precludes taking individual specimens for diet assessment based on analysis of stomach contents. In any event, this method yields only a small number of samples (Bent 1929). Also the organisms on which this bird feeds are small, and identifying prey consumed by direct visual observation is difficult (Cairns 1977). Examination of the abundance and diversity of organisms present in the habitat allows inferences to be drawn regarding the prey likely to be in the Piping Plover's diet (Whyte 1985, Nordstrom 1990).

Fecal analysis offers an alternative to the usual techniques in determining diets of Piping Plovers. This technique has been used for the Dunlin (*Calidris alpina*), the Black-bellied Plover (*Pluvialis squatarola*) (Le V. Dit Durell and Kelly 1990), and for a small sample (24 droppings) of the Piping Plover (Nicholls 1989).

METHODS

In the summers of 1990–1992 130 droppings were collected at four sites on the Magdalen Islands, Quebec, Canada (47°24′N; 61°48′W): on the lagoon beaches of the West Dune and Hospital Beach, which are situated on the shore of the Havre aux Basques and Havre aux Maisons lagoons, respectively, and on the ocean beaches of the West Dune and South Dune. The birds were observed by telescope (22×) to determine when they defecated. The droppings were then collected and preserved in 70% alcohol. At other times, droppings were found by following the bird's tracks, easily recognizable in the sand. Since plover families

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TABLE 1
INVERTEBRATES FOUND IN DROPPINGS OF PIPING PLOVERS

Organisms	Frequency (%)			
	West Dune		Hospital Beach	South Dune
	Lagoon side N = 44	Ocean side N = 53	Lagoon side N = 18	Ocean side N = 15
Gastropoda	20.5	1.9	5.6	0.0
Amphipoda	2.3	28.3	<0.1	<0.1
Cicindelidae	4.5	5.7	0.0	6.7
Carabidae	0.0	1.9	5.6	0.0
Staphylinidae	54.5	17.0	77.8	66.7
Curculionidae	6.8	45.3	94.4	33.3
Coleoptera (larvae)	52.3	0.0	5.6	13.3
Coleoptera (spp.)	6.8	67.9	22.2	20.0
Diptera	25.0	41.5	22.2	26.7
Diptera (larvae)	29.5	0.0	0.0	0.0
Hymenoptera	0.0	1.9	0.0	0.0

do not forage far afield, we assumed that the invertebrates found in the droppings were from the same habitat as where they were collected. The contents of the feces were identified using a stereoscopic microscope. Invertebrate fragments were identified as accurately as possible by comparison with a reference collection of whole specimens gathered on the feeding sites.

In order to build this reference collection and evaluate prey availability on the beaches, 140 soil samples were taken. A cylinder capable of holding a sample of 362 cm^3 was inserted to a depth of 5 cm. The material retrieved was screened on the spot (mesh: 500 μm), and the organisms obtained were preserved in 70% alcohol for identification in the laboratory. The sampling was done at sites that support the feeding of families of Piping Plover. The samples were taken a short time after the young fledged to avoid disturbing families and to obtain invertebrates representative of those they consumed.

RESULTS

Among the organisms found in the Piping Plover's droppings, insects were well represented, especially four different families in the order Coleoptera (Table 1). The hard body of the beetle is very resistant to damage in the bird's digestive tract, making identification in the feces easy. Nonetheless, this list is incomplete. Soft-bodied organisms leave no identifiable parts in the droppings, which probably explains the absence of worms from this list. Certain invertebrate fragments also remained unidentifiable.

Staphylinidae (43.8%), Curculionidae (31.5%), and Diptera (31.5%) were the invertebrates most often found in the feces of the Piping Plover (Table 2). Significant differences were found between the prey consumed, depending on the site used. There were more Coleoptera larvae (χ^2 = 11.8, df = 1, $P \leq 0.001$) and Diptera larvae (χ^2 = 6.7, df = 1, $P \leq$

TABLE 2
COMPARISON OF INVERTEBRATES FOUND IN DROPPINGS AND SOIL ON FEEDING GROUNDS OF THE PIPING PLOVER

Organisms	Frequency (%)	
	Feces N = 130	Soil N = 140
Gastropoda	8.5	4.2
Oligochaeta	0.0	5.7
Amphipoda	16.9	2.1
Collembola	0.0	2.1
Cicindelidae	4.6	0.0
Carabidae	1.5	0.0
Staphylinidae	43.8	37.1
Curculionidae	31.5	0.0
Coleoptera (larvae)	20.0	42.1
Coleoptera (spp.)	35.4	0.0
Trichoptera (larvae)	0.0	1.4
Diptera	31.5	0.7
Diptera (larvae)	10.0	20.0
Hymenoptera	0.8	0.7

0.001) in the feces found on the lagoon beaches of the West Dune than at Hospital Beach. Conversely, Curculionidae were more abundant in the feces gathered from Hospital Beach ($\chi^2 = 44.9$; df = 1, $P \leq 0.001$). This difference illustrates the diversity of organisms found in the lagoons of Havre aux Basques and Havre aux Maisons. A comparison of the organisms found in the droppings collected on the ocean beaches of the West Dune and the South Dune revealed that there were more Staphylinidae in the feces found at the South Dune ($\chi^2 = 14.3$, df = 1, $P \leq 0.001$). The differences between the other organisms either were insignificant or the samples were too small to apply a statistical test.

For the West Dune, we compared samples taken from the ocean side and the lagoon side of the same dune and found a significant difference between the frequency of Staphylinidae ($\chi^2 = 15.1$, df = 1, $P \leq 0.001$), Coleoptera larvae ($\chi^2 = 36.3$, df = 1, $P \leq 0.001$) and Diptera larvae ($\chi^2 = 18.1$, df = 1, $P \leq 0.001$) present in the feces collected from the lagoon side. In the feces from the ocean side of this dune, Amphipoda ($\chi^2 = 11.8$, df = 1, $P \leq 0.001$) and Curculionidae ($\chi^2 = 17.7$, df = 1, $P \leq 0.001$) were found most frequently.

Abundance of most prey items cannot be determined precisely by fecal analyses. An estimate of the quantities ingested is possible for some hard-bodied organisms. Elytra of Staphylinidae remain intact in

the feces, for example, and can be counted. The same is true for heads of Curculionidae and Coleoptera larvae. Counts based on droppings collected in 1992 (N = 60) revealed that an average of 14.9 Staphylinidae was present in each fecal sample. Staphylinidae were not only frequent in the droppings but also abundant in the diet. The Piping Plover eats relatively smaller quantities of Coleoptera larvae and Curculionidae since the average number of these specimens was 2.8 and 1.7 per sample, respectively.

Contents of 25 droppings from nestlings between 13 and 18 days of age included Staphylinidae (64%), Diptera (36%), and Curculionidae (32%). Nestlings also ate Coleoptera larvae (28%), Gastropoda (16%), Diptera larvae (12%), and Amphipoda (8%). Due to the small number of fecal samples of adult origin (N = 7), it was difficult to compare the diets of the young birds and adults.

Comparison of the frequency of prey in the droppings with the frequency of invertebrates present in the soil samples gives a picture of the Piping Plover's prey selection (Table 2). Oligochaeta and the larvae of Diptera and Coleoptera were more frequent in the soil samples than in the feces. On the other hand, Coleoptera, Amphipoda, Diptera, and Hymenoptera were most common in the fecal samples. These invertebrates, in contrast to the preceding group, inhabit the beach surface and thus are easier for the plover to find. Two biases should be kept in mind when analyzing this table. First, soft-bodied prey, such as Oligochaeta, which have a high degree of digestibility (Swanson and Bartonek 1970), leave no easily identifiable traces, which leads to an underestimation of the frequency of these organisms in the feces. Second, the technique used for taking soil samples does not permit adequate sampling of the most mobile organisms.

DISCUSSION

Use of feces as a method for analyzing diet of the Piping Plover gives a qualitative determination of the list of organisms collected in the habitat and, for several prey items, a quantitative analysis. Despite the difficulties in identifying certain invertebrate fragments and finding traces of soft-bodied invertebrates, fecal analyses made it possible to establish the presence of Gastropoda, Amphipoda, Coleoptera (Cicindelidae, Carabidae, Staphylinidae, Curculionidae), Diptera, and Hymenoptera in the Piping Plover's diet. Staphylinidae are an important group of organisms in this diet. These insects are specially adapted for life in a marine habitat; the adults and larvae can survive a long time buried in the sand when salt water covers the beach. When the water recedes, they come

out to feed on diatoms (Griffiths and Griffiths 1983). They are thus most often found on the lagoon side where the sand is more exposed.

There is no reason to believe that the diet of the young differs from that of the adults since they feed in the same way at the same sites. It is possible, however, that nestlings only a few days old are unable to capture the faster-moving insects such as Diptera or Cicindelidae.

The absence of marine worms from feces in this study may be because our technique is ineffective in identifying soft-bodied organisms. However, marine worms are scarce in the Magdalen Islands. Only 5.7% of the 140 soil samples taken contained worms. Oligochaeta found were also very small and probably are not eaten by the plover. Doyon and McNeil (1978) analyzed the stomach contents of 159 birds of the family Scolopacidae in Havre aux Basques and found only a single Oligochaeta despite the abundance of this worm in the soil samples they collected from the feeding grounds.

Unlike other shorebird species, the Piping Plover is a surface feeder. Organisms found in the droppings are principally adult organisms living at the beach surface, which suggest that the Piping Plover finds its prey by sight. The movement and size of these organisms probably attract the bird's attention, leading to their capture. Prey buried in the ground are less visible to the plover and are eaten only occasionally or when the bird taps the ground with its foot to make the organism come out on the surface (Cairns 1977).

The Piping Plover requires feeding grounds rich in surface invertebrates. There is some evidence to suggest that motor vehicle traffic on beaches reduces the abundance of available invertebrates (Wheeler 1979). This factor also decreases the feeding time, which reduces the productivity of Piping Plover pairs (Flemming et al. 1988).

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BREEDING BIOLOGY OF HOUSE SPARROWS IN NORTHERN LOWER MICHIGAN

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Abstract.—The breeding biology of the House Sparrow (*Passer domesticus*) in northern lower Michigan was monitored during the summers of 1986–1991 and the results compared to those obtained in other North American studies. Individuals are multi-brooded with most females laying two or three clutches per year. Overall mean clutch size for the periods of observation was 4.96, and declined as the season progressed. Hatching was asynchronous and indicated that incubation began between the laying of the antepenultimate and penultimate eggs. A strong, positive correlation of mean clutch size with latitude was noted. Incubation period, nestling period, hatching success, fledging success and overall nesting success in Michigan were similar to those found in other North American studies. No latitudinal trends were detected in any of these reproductive characteristics. In a comparison of the timing of the initiation of first and second clutches in North America, however, a strong latitudinal trend was observed, suggesting a retardation of approximately two days in the timing of breeding for each 1° of latitude poleward. *Received 20 Sept. 1993, accepted 1 Dec. 1993.*

The House Sparrow (*Passer domesticus*), indigenous throughout most of Europe, Asia, and northern Africa, has been successfully introduced into North America, South America, Australia, and southern Africa (as well as numerous islands throughout the world) and is now perhaps the most widely distributed avian species. It was introduced into the eastern United States and Canada repeatedly from 1853 to approximately 1881 (Barrows 1889) and extended its range steadily and rapidly across the United States and Canada (Wing 1943). It is now an abundant resident throughout the continental United States, the southern tier of Canadian provinces, and throughout Central America locally as far south as Panama (Lowther and Cink 1992). The House Sparrow is a common resident throughout Michigan, but breeds at much lower densities in the upper peninsula and the northern half of the lower peninsula than in the southern half of the lower peninsula (Brewer et al. 1991). Several studies on the breeding biology of the House Sparrow in various parts of its North American range have been published (i.e., Weaver 1942; Will 1973; Pitts 1979; McGillivray 1981, 1983). No comprehensive study of the species appears to have been undertaken in Michigan, however. The present study reports on aspects of the breeding biology of the House Sparrow in northern lower Michigan.

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METHODS

The study area consisted of three occupied farmsteads (four in 1986) near the Univ. of Michigan Biological Station (UMBS), Cheboygan County, Michigan. The three sites were active dairy farms with numerous barns and sheds, while the one additional site used in 1986 was an occupied but inactive farmstead with no stock maintained on the premises. No nest-boxes were present at any of the study sites in 1986 so that all House Sparrow nests under observation in that year were located in crevices in buildings (both outside and inside the buildings), in holes in trees, or in the branches of trees. Fifteen next-boxes were placed on buildings and trees at each of the three sites in March 1987 and many of the nests observed in 1987–1991 were located in nest-boxes.

The periods of observation in the six years were 7 June to 10 August 1986 (except for a 6-day hiatus from 12–17 July), 4 June to 17 August 1987, 13 June to 13 August 1988, 12 June to 12 August 1989, 18 June to 12 August 1990, and 16 June to 15 August 1991. The periods of observation mean that only partial or no data were collected on first broods at the sites, a fact which may affect some of the comparisons below. Active nest sites were visited daily (normally between 07:00 and 11:00 h EDT) during the egg-laying period (until the clutch was complete) and from late in the incubation period throughout the nestling period until fledging. Visits were made at three- or four-day intervals during incubation. Eggs were numbered with a felt-tip pen and were weighed and measured on the day of laying. Nestlings were individually marked on the day of hatching by toenail clipping and were banded with U.S. Fish and Wildlife Service bands at 10 days. After the nestlings were 11 or 12 days old, they were not handled or counted to avoid premature fledging. Fledging date was determined by noting the day on which no nestlings remained in the nest, and all young banded were assumed to have fledged unless found dead in the nest-box. Females were captured at nest-box nests when the oldest nestlings were five days old, and tarsus length was measured with dial calipers, flattened wing chord was obtained with a metric rule, and mass was measured with a 50-g Pesola balance. All females were also banded with a USFWS band. Interbrood intervals, the number of days from the fledging of one brood to the initiation of the next clutch, were determined for 50 marked females in 1987–1991 (some of which reared experimentally manipulated broods).

Utilizing the modal values observed in this study for clutch size (5), incubation period (12 days), and nestling period (14 days), the date of initiation was estimated for all clutches in which it was not directly observed. Due to the fact that observations were not begun until early- to mid-June, most first clutches were missed. The first fledgling flocks (flocks formed as fledglings become independent of parental feeding about 7–10 days post-fledging [pers. obs.]) were not observed before about 10–15 June, however, which indicates that the peak of first clutch initiations did not occur until about 1 May. A marked peak in clutch initiation occurred in the 10–19 June interval in each year of the study, which undoubtedly corresponded to the peak period of initiation of second clutches. Based on an inspection of the daily progression of clutch initiations, I decided to consider 27 May as the first date on which "second clutches" could be initiated following the successful fledging of a first brood and arbitrarily considered clutches initiated after that date to be "second broods". Clutches initiated after 2 July were considered "third broods".

In 1989–1991, brood sizes of 41 "second broods" were manipulated at hatching to create supernormal- and subnormal-sized broods. Nestlings were removed from one nest when 0 or 1 day old and added to other nests with young of the same age to create broods of 7–9 young (each supernormal brood contained at least one and as many as three more young than the clutch size of the nest). Data from these manipulated broods and other experimentally manipulated nesting attempts (see Anderson 1989) are not included in the analyses

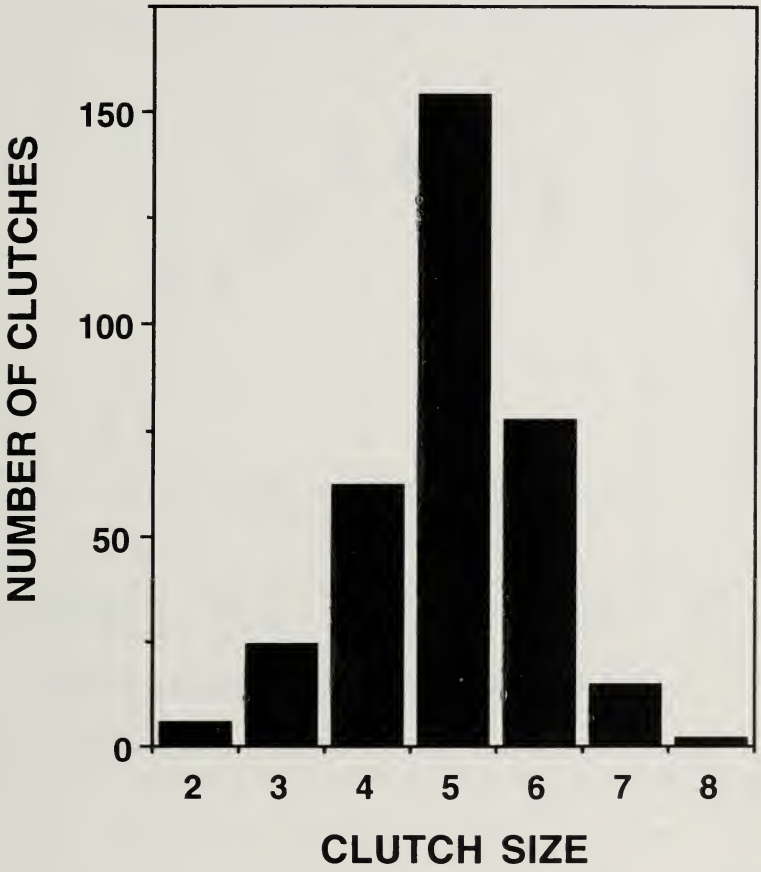

FIG. 1. Frequency distribution of clutch size of the House Sparrow in northern lower Michigan, 1986–1991 (N = 340).

below, except as noted. Frequent handling of eggs and young resulted in some egg breakage and nestling mortality. Observer-related mortality, either accidental or experimental, is not included in the analyses that follow.

RESULTS AND DISCUSSION

Clutch size varied from 2 to 8 with a strong mode of 5 and a mean of 4.96 (SE = 0.06, N = 340) (Fig. 1). Mean clutch size varied considerably among years, from a mean of 4.58 in 1986 to a mean of 5.18 in 1988 and 1990, with the differences among years being significant (one-way ANOVA, $F_{5,334} = 4.56$, $P < 0.001$). Clutch size also varied seasonally with a marked decrease in mean clutch size for clutches initiated in late July and August (Fig. 2). Analysis of covariance (with period of initiation

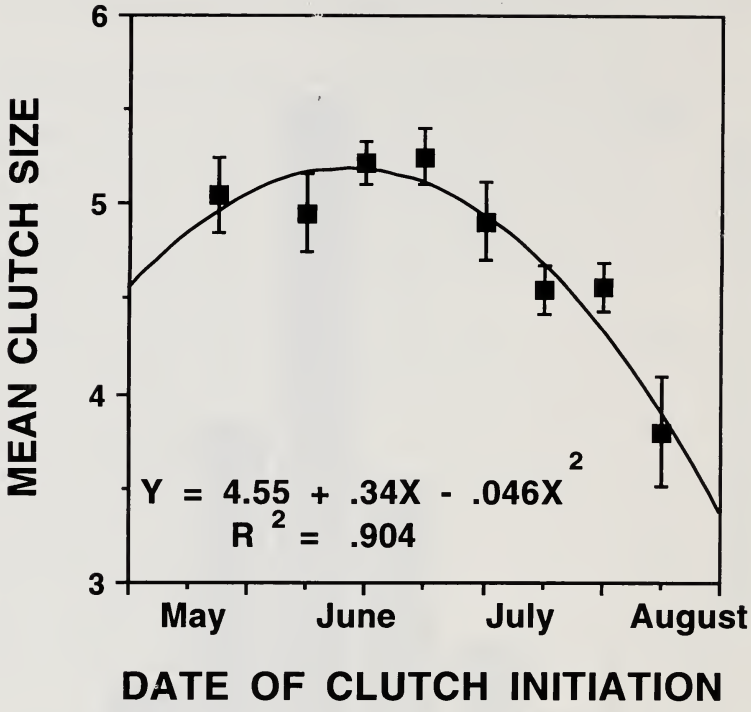

FIG. 2. Seasonal change in mean clutch size of the House Sparrow in northern lower Michigan. (Data plotted as mean ± SE for ten-day intervals beginning with interval 1 = May 11–20.)

as a covariate and ignoring clutches initiated in May because of lack of data for some years) still resulted in significant annual variation in clutch size ($F_{5,311} = 4.73$, $P < 0.001$). No significant interaction between year and initiation period was observed, however ($F_{5,306} = 0.45$, $P > 0.80$), suggesting that the slope of the seasonal change in clutch size did not change with year. A similar decrease in clutch size has been noted in Great Britain (Seel 1968), and at other locations in North America (Will 1973, Anderson 1978). Due to the fact that observations were not begun until early- or mid-June, very little data are available for clutches initiated before mid-May. This, plus the marked decrease in clutch size near the end of the breeding season, suggests that the observed overall mean clutch size may be lower than the true mean for the entire breeding season, a fact which complicates comparison with other North American studies. Data from other North American studies of the House Sparrow are summarized in Table 1. Mean clutch size shows a strong positive correlation

TABLE 1

SUMMARY OF DATA ON BREEDING BIOLOGY OF THE HOUSE SPARROW IN NORTH AMERICA

Location (Latitude)	Mean clutch size	Mean incubation period (days)	Mean nestling period (days)	Hatching success	Fledging success	Nesting success	Source
Mississippi State, Mississippi (33°28′N)	3.93*	12.2	17.1	0.832[a]	0.770	0.641[a]	Sappington 1975, 1977
Plainview, Texas (34°10′N)	4.23*	11.3	n.a.	0.596*	0.534*	0.318*	Mitchell and Hayes 1973, Mitchell et al. 1973
Stillwater, Oklahoma (36°07′N)	4.47	n.a.	13.9	0.502*	0.649*	0.326*	North 1968
Martin, Tennessee (36°20′N)	4.67	11.8	14.6	0.515	0.654	0.337	Pitts 1979
McLeansboro, Illinois (38°05′N)	4.46	n.a.	n.a.	0.658[a]	0.533	0.351[a]	Will 1973
Portage des Sioux, Missouri (38°55′N)	4.64	n.a.	14.8	0.646	0.628	0.406	Anderson 1978
Lawrence, Kansas (39°02′N)	5.14	11.76	13.91	0.625[a]	0.646	0.404*[a]	Lowther 1979a, 1983
Ithaca, New York (42°26′N)	4.73	n.a.	14.4	n.a.	n.a.	0.705[a]	Weaver 1942, 1943
Coldspring, Wisconsin (43°00′N)	4.96	11.7	15.4	0.508*	0.612*	0.311*	North 1972
Pellston, Michigan (45°32′N)	4.96[b]	11.55	14.3	0.717	0.779	0.559	This study
Calgary, Alberta (51°05′N)	5.03*	n.a.	n.a.	0.698*[a]	0.665*	0.464*[a]	Murphy 1978

* Calculated from data presented in the source(s).
n.a. = data not available.
[a] Based on completed clutches only.
[b] Based on only part of the breeding season.

with latitude ($r = 0.757$, $P < 0.01$). Murphy (1978) and Anderson (1973, 1978) also noted significant positive correlations between latitude and clutch size in North American populations of the House Sparrow.

The curvilinear regression equation relating mean clutch size (Y) to latitude (X) explained a higher proportion of the variation of clutch size (multiple $R = 0.863$) with both the X and X^2 terms contributing significantly to the regression ($t = 2.56$, $P < 0.05$ and $t = 2.29$, $P = 0.05$, respectively): $Y = -6.20 + 0.48X - 0.005X^2$. This suggests that there is a damping of the rate of increase in clutch size with increasing latitude at more northern latitudes in North America. Incubation period, defined as the period from the laying of the last egg in a clutch until the hatching of that egg (Thomson 1964), varied from 10 to 13 days with a mode of 12 (mean = 11.55, SE = 0.05, N = 119). This is very close to the mean incubation period in other North American studies of the species (Table 1). No correlation was found between latitude and mean incubation period ($r = -0.280$, $P > 0.55$).

At least one egg hatched in 81.3% of the 316 nests for which hatching data were available. No significant differences were observed among years in the proportion of nesting attempts in which eggs hatched ($\chi^2 = 6.54$, $P > 0.10$). Hatching success, defined as the percentage of eggs laid (including eggs from nests in which the clutch was deserted or lost prior to completion) which hatched successfully was 71.7% (N = 1457 eggs). Hatching success in other North American studies has ranged from 50.8% in Coldspring, Wisconsin (North 1972) to 83.2% in Mississippi State, Mississippi (Sappington 1977) (Table 1). Note that some studies, including Sappington's (1977), calculated hatching success based on completed or incubated clutches only, ignoring losses of eggs in attempts which failed prior to clutch completion, which means that all of the hatching success values in Table 1 are not strictly comparable. This discrepancy is, however, not too great in that these losses normally involve only one or two eggs from a small percentage of the total breeding attempts. The average hatching success for all North American studies, including the present study (each taken as a single data point regardless of sample size), is 63.0%. No latitudinal trend in hatching success is detectable ($r = 0.115$, $P > 0.75$).

Hatching was asynchronous, requiring more than one day in most nests (Table 2). In 210 nests in which two or more chicks hatched the mean hatching interval was 1.31 days (SE = 0.05). Hatching interval did not differ significantly with clutch size (ANOVA, $F_{4,204} = 1.73$, $P > 0.10$), although it did differ significantly with number hatching (ANOVA, $F_{5,204} = 3.87$, $P = 0.002$). Sappington (1975) reported a mean hatching interval of 0.35 days for the House Sparrow in Mississippi, while Seel (1968)

TABLE 2
MEAN HATCHING INTERVALS OF HOUSE SPARROWS IN NORTHERN LOWER MICHIGAN

Number of young hatching	Number of nests	Mean hatching interval[a] (days)
2	14	0.71 (0.73)[a]
3	28	1.07 (0.77)
4	66	1.30 (0.66)
5	69	1.44 (0.70)
6	29	1.55 (0.74)
7	4	1.50 (0.58)

[a] Hatching interval was estimated for each nest by assuming that the young that had hatched since the last nest check 24 h earlier had hatched at the midpoint between the two nest checks. Therefore, the estimated hatching interval for a nest was one day less than the number of days over which hatching was observed. Numbers in parentheses are one standard error.

reported a mean hatching interval varying from 1.17 days for two-egg clutches to 2.00 days for six-egg clutches in Great Britain.

The nestling period lasted from 11 to 18 days with a mean duration of 14.3 days (SE = 0.10, N = 137). Manipulated broods from 1989–1991 are included as nestling period did not differ significantly among reduced, control, and supernormal broods (Anderson, unpubl. data). In a two-way ANOVA, nestling period did not differ annually ($F_{5,125} = 0.38$, $P > 0.85$), with brood (for "second" and "third" broods, $F_{1,125} = 0.41$, $P > 0.50$), or with the interaction of year and brood ($F_{5,125} = 0.37$, $P > 0.85$). The mean nestling period noted in other North American studies varied from 13.9 to 17.1 days (Table 1). No correlation of mean nestling period with latitude was observed ($r = -0.398$, $P > 0.30$).

At least one young fledged from 87.9% of the 232 nests in which eggs hatched and for which complete data were available. Fledging success, defined as the percentage of eggs hatched which resulted in fledged young, was 77.9% (N = 719 hatched eggs). Broods involved in brood-size manipulation experiments in 1989–1991 (both reduced and supernormal broods) were not included in this analysis. Fledging success in nine other North American studies varied from 53.3% in McLeansboro, Illinois (Will 1973) to 77.0% at Mississippi State (Sappington 1977) (Table 1). No correlation was noted between fledging success and latitude ($r = 0.219$, $P > 0.50$). Mean fledging success for the ten North American studies was 64.7%.

Nesting success, the proportion of eggs laid which result in successfully fledged young, can be estimated by taking the product of hatching success and fledging success. Nesting success in the present study was 55.9%. Nesting success in ten other North American studies varied from 31.1% at Coldspring, Wisconsin (North 1972) to 70.5% at Ithaca, New York

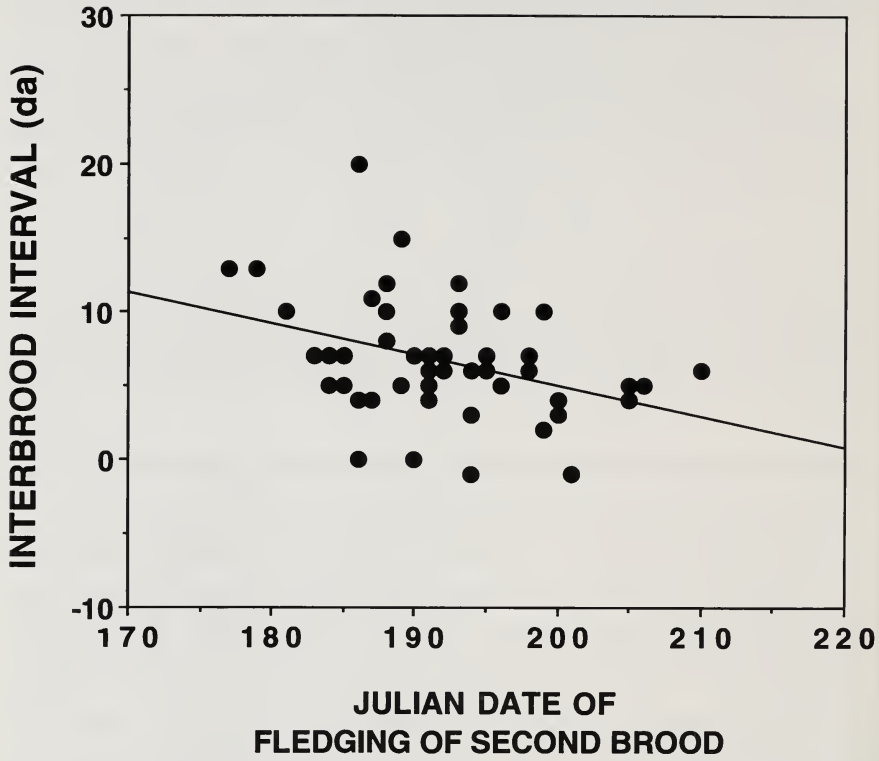

FIG. 3. The relationship between date of fledging of the second brood and the interbrood interval (days from fledging of one brood to initiation of egg-laying in subsequent clutch) for 50 marked females laying third clutches, 1987–1991 ($r = -0.367$, N = 50, $P < 0.01$).

(Weaver 1942) (Table 1), and the mean nesting success for all the studies was 43.8%. No relationship was found between nesting success and latitude ($r = 0.225$, $P > 0.50$).

The interbrood interval between "second" and "third" broods of 50 marked females varied from −1 to 20 days (mean = 6.68 days, SE = 0.57). In two instances the female began her "third clutch" one day before the "second brood" young fledged (once in the same nest and once in a nearby site). In two other instances, the female began laying on the day the young fledged. Such brood overlap has previously been reported in the House Sparrow (Lowther 1979b). There was a strong mode of clutch initiation 4–7 days after fledging of the "second brood" with 30 (60%) of the marked females having interbrood intervals in that range. Interbrood interval did not vary significantly among years of the study (ANOVA, $F_{4,45} = 0.952$, $P > 0.40$), with initial brood size ($r =$

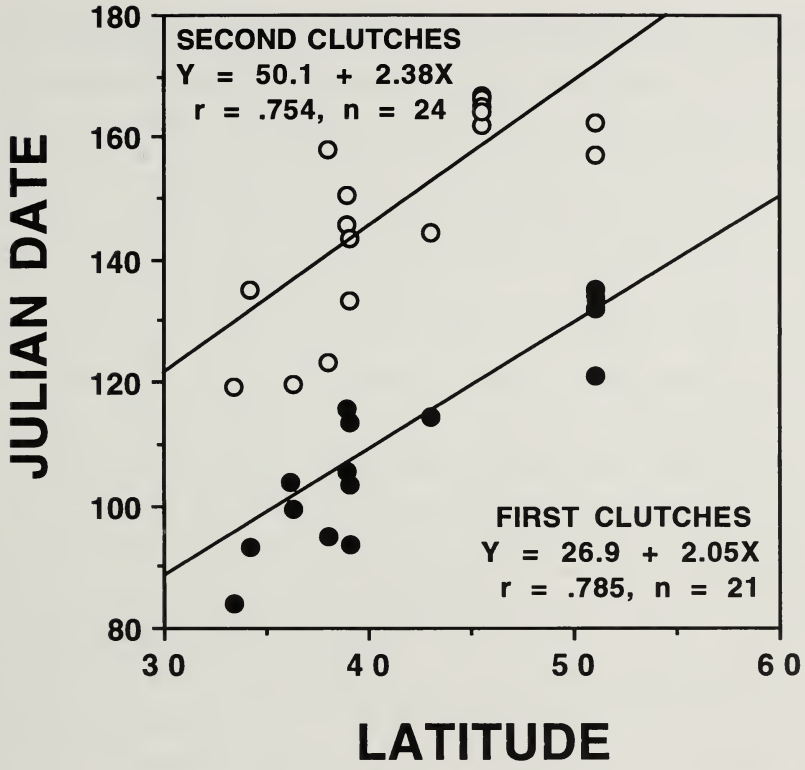

FIG. 4. The relationship between latitude and the peak initiation dates of first and second clutches of the House Sparrow in continental North America. Most dates are midpoints of modal periods of clutch initiation, although some are mean or median dates. Data were obtained from the following sources (Anderson 1973, unpubl. data; Lowther 1979a; McGillivray 1983; Mitchell et al. 1973; Murphy 1978; North 1968, 1972; Pitts 1979; Sapington 1977; Will 1973).

0.174, N = 48, $P > 0.20$), or with the number of young fledging from second broods ($r = 0.195$, N = 50, $P > 0.15$) (in all cases supernormal broods were included). In 1989–1991, interbrood interval did not differ significantly between females that reared supernormal "second broods" (mean = 7.17 days, SE = 1.30) and control females (mean = 6.96 days, SE = 0.93) ($t_{34} = 0.13$, $P > 0.85$). Interbrood interval did show a significant negative relationship with the fledging date of the "second brood" ($r = -0.367$, N = 50, $P < 0.01$) (Fig. 3).

Peak dates of initiation of first and second clutches in North American studies are plotted against latitude in Fig. 4 (in most cases the peak date is the midpoint of an interval in which the peak numbers of clutches were

initiated). The correlations between peaks of both first and second clutches and latitude are highly significant ($r = 0.785$, $P < 0.01$ and $r = 0.754$, $P < 0.01$). The least squares linear regression equations for the data are also presented in Fig. 4. The slopes of both of the regression lines are close to 2 (2.05 and 2.38) suggesting that there is a delay in the chronology of breeding among North American populations of the House Sparrow of approximately two days for each degree of latitude poleward. A similar retardation with latitude was noted for the date of initiation of first clutches at 20 sites in Asia, Europe and North America (the slope of the regression equation was 1.94, Dyer et al. 1977). This is only half of the four-day retardation observed in the phenology of plants and arthropods (Hopkins 1938), and may be reflective of the effect of endothermy on breeding phenology. It may also reflect in part the adaptive physiological differences among House Sparrow populations observed by Hudson and Kimzey (1966). Threadgold (1960) observed a retardation in the onset of spermatogenesis with increasing latitude in North American populations of the House Sparrow, but the number of locations, four, was insufficient to perform meaningful quantitative comparisons. In a comparative study of coastal populations of the Song Sparrow (*Melospiza melodia*), Johnston (1954) found a three to four day retardation in the onset of breeding for each degree of latitude. A considerable amount of annual variation in the timing of the peaks of first and second clutches at some locations is also evident in Fig. 4. This variation is apparently due primarily to annual variation in local climatic conditions (i.e., early or late springs).

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SHORT COMMUNICATIONS

Diurnal time budgets of Common Goldeneye brood hens.—Egg production and incubation by female waterfowl have high energetic and nutrient costs (Alisauskas and Ankney 1992, Afton and Paulus 1992). As a consequence, female body mass and condition at the end of incubation are often at or near their lowest points of the year. Thus, the brood-rearing period is important, as females must care for their young while regaining their body condition and preparing to molt. Although waterfowl studies (Lazarus and Inglis 1978, Afton 1983, Rushforth Guinn and Batt 1985) have used descriptive data collected from brood hens to test various aspects of parental investment theory (Trivers 1972), data for many species have not been collected, and factors affecting parental investment are not well known.

We studied time-activity budgets of Common Goldeneye (*Bucephala clangula*) females with broods because this aspect of their biology has received little attention. Our objective was to describe time-activity budgets of Common Goldeneye brood hens. Lakes that are used most for nesting and brood rearing in north-central Minnesota also support highly productive populations of fish. This contrasts with other locations where fishless lakes or those having few fish have been reported as being most important for brood rearing and where goldeneyes are believed to compete with fish for invertebrate foods (Eriksson 1979, Eadie and Keast 1982, Blancher et al. 1992, and others). Our data should add to the understanding of waterfowl parental investment and fish competition in Common Goldeneyes.

Study area and methods.—Brood hen time-activity budgets were studied on two north-central Minnesota lakes in 1984 and 1985. Island Lake (1250 ha) had moderate to heavy year-round and summer residential shoreline development. Shoreline and mid-lake stands of hardstem bulrush (*Scirpus acutus*) and reed grass (*Phragmites communis*) were extensive, and 39% of the basin was <3 m in depth. Each year, 30–35 goldeneye broods occupied the lake. Lake Bemidji (2600 ha) had heavy residential shoreline development. Shoreline stands of emergent vegetation were limited, and 29% of the basin was <3 m in depth. Approximately 20 goldeneye broods occupied the lake. Fish communities in both lakes were dominated by populations of Percidae and Esocidae, and fishing and boating were intensive beginning in May. Recreational boating was more prevalent on Lake Bemidji. Morpho-edaphic indices (MEI) (Ryder 1965) were 18.01 and 8.72 for Island Lake and Lake Bemidji, respectively (Minn. Dep. Nat. Resour., Section of Fisheries, unpubl. data). These MEI values are near optimum for highly productive fish communities (Ryder et al. 1974).

Activities of unmarked females with broods were sampled using the focal animal method (Altmann 1974) and 1-h observation sessions. The period from 0.5 h before sunrise to 0.5 h after sunset was divided into four equal-length blocks that were adjusted daily to account for changing day length. For each block, a random start time was selected such that the latest possible start would be 1 h before the end of the time block. We tried to minimize any systematic bias in our sample by alternately using access points at opposite ends of the lakes and also alternating the directions travelled from the access points to locate broods. We sampled the first brood hen encountered after determining the random start time and sequentially sampled as many as we could thereafter in the time block. Usually little time elapsed between independent samples as two or more broods sometimes could be observed without moving our boat. Broods were aged according to plumage development (Gollop and Marshall 1954).

Activities were recorded every 30 sec using a metronome (Weins et al. 1970) and categorized as (1) foraging (dive, dive-pause, food sorting at the surface), (2) alert, (3) locomotion, (4) agonistic (surface-threats, shallow dive-threats, fights) (see Savard 1984, 1988),

Table 1

Percent of Diurnal Time Spent in Various Activities by Common Goldeneye Brood Hens in Northcentral Minnesota, 1984–1985[a]

		Brood size			
		Small		Large	
Activity	Lake	1984	1985	1984	1985
Alert	Island	36.9 (4.0)[b]	33.9 (3.6)	32.0 (5.8)	36.7 (4.7)
	Bemidji	20.4 (3.6)	28.5 (2.7)	26.1 (9.0)	28.7 (2.7)
Foraging	Island	18.9 (3.8)	15.9 (2.4)	11.8 (2.6)	26.2 (3.5)
	Bemidji	20.4 (4.1)	23.0 (4.1)	28.3 (8.0)	28.4 (3.7)
Locomotion	Island	11.8 (1.8)	12.0 (1.6)	20.7 (3.5)	12.9 (1.8)
	Bemidji	11.9 (2.1)	10.5 (2.3)	37.3 (2.0)	17.2 (2.5)
Resting	Island	7.3 (2.2)	17.5 (3.7)	19.5 (4.3)	10.8 (4.5)
	Bemidji	19.2 (6.2)	22.3 (5.9)	4.8 (4.8)	14.5 (3.9)
Comfort	Island	21.1 (3.2)	12.6 (1.5)	15.2 (2.6)	9.9 (1.8)
	Bemidji	17.7 (2.5)	11.0 (2.1)	2.3 (0.4)	8.4 (1.6)
Left brood	Island	3.5 (2.7)	3.2 (1.7)	0.0 (0.0)	1.9 (1.9)
	Bemidji	3.6 (3.6)	3.1 (2.2)	0.0 (0.0)	1.6 (0.8)
Agonistic	Island	0.6 (0.3)	4.9 (2.2)	0.8 (0.4)	1.6 (1.0)
	Bemidji	6.7 (2.6)	1.7 (0.9)	1.1 (0.6)	1.1 (0.3)

[a] Island Lake sample size (1984 = 27 h, 1985 = 51 h), Lake Bemidji sample size (1984 = 16 h, 1985 = 38 h).
[b] Mean (SE).

(5) comfort movements, (6) resting, (7) away from brood, or (8) out of sight. Observation sessions were analyzed if females were visible for ≥ 30 min. Activities were summarized as the percent of the session that they comprised while the bird was in sight. We collapsed activities into categories of parental care (alert, locomotion, and agonistic) and self-maintenance (foraging, comfort, and resting) in a fashion similar to Rushforth Guinn and Batt (1985) except that we also considered foraging dive-pauses to be parental care and away from brood to be self-maintenance. We recognize, as have others, that any one activity may not exclusively serve one category or the other.

Effects of location, year, brood age (class I or II), brood size (<7 or ≥7 ducklings), and their interaction on percent time spent in each activity were examined using a two-way factorial ANOVA on the arcsine-transformed data. We set our significance level at $\alpha = 0.05$. We maintained the overall α level in analyses having ≥ three response variables by preceding the ANOVAs with a single two-way factorial MANOVA on the transformed data using SAS PROC GLM (SAS Institute Inc. 1991). When interactions were not significant, we repeated the MANOVA using the reduced model. Significant multivariate main effects were followed by their corresponding univariate ANOVAs.

Results.—Hens with broods were observed for a total of 132 hours. Observations were reasonably well-balanced among time blocks within lakes and years. Wilk's Lambda test criterion indicated that no interaction among year, location, brood age, or brood size was significant (all P values > 0.16). For the main effects model, location, year, and brood size influenced activity budgets (MANOVA $F = 2.76$; df = 7, 121; $P = 0.011$; $F = 2.27$; df = 7, 121; $P = 0.033$; and $F = 2.95$; df = 7, 121; $P = 0.007$, respectively), but brood age did not ($P = 0.812$). Brood hens spent most of the diurnal period alert and foraging (Table 1). Females on Island Lake were alert more often than those on Lake Bemidji ($F = 8.00$; df

TABLE 2

PERCENT OF DIURNAL FORAGING TIME SPENT IN VARIOUS ACTIVITIES BY COMMON GOLDENEYE BROOD HENS IN MINNESOTA, 1984–1985[a]

Activity	Brood age	
	Class I (N = 63 h)	Class II (N = 69 h)
Diving	82.9 (2.8)[a]	92.0 (2.4)
Pausing	8.8 (1.5)	2.8 (0.9)
Sorting	8.3 (2.4)	5.2 (2.2)

[a] Mean (SE).

= 1, 127; $P = 0.005$), and they foraged less ($F = 5.83$; df = 1, 127; $P = 0.017$). We detected no other behaviors that were influenced by location (all P values > 0.17). Time spent in locomotion and in comfort behaviors were the only times affected by year, and both were generally greater in 1984 than 1985 ($F = 4.21$; df = 1, 127; $P < 0.042$; $F = 11.96$; df = 1, 127; $P < 0.001$; all other P values > 0.17). Hens accompanying small broods spent more time in comfort activities and less time moving than those with large broods ($F = 6.34$; df = 1, 127; $P = 0.013$ and $F = 11.72$; df = 1, 127; $P < 0.001$). Brood size had no effect on any other behavior (all P values > 0.05). Brood females spent comparable amounts of time resting, in locomotion, and in comfort activities. Time away from the brood and in agonistic activities were the least observed.

Most foraging time was spent in underwater dives and the least in sorting items at the surface and pausing between dives (Table 2). For the main effects model, brood age was significant (MANOVA $F = 7.47$; df = 3, 113; $P < 0.001$), but other factors were not (all P values > 0.19). Hens accompanying younger broods spent less time in dives and more time pausing between dives ($F = 12.19$; df = 1, 115; $P < 0.001$ and $F = 13.70$; df = 1, 115; $P < 0.001$), but we detected no difference in the proportion of time they spent sorting food at the surface ($P = 0.72$).

We detected no influence from year, location, brood age, or brood size on the proportion of agonistic activity directed at other goldeneyes versus non-goldeneye hens (all P values > 0.12). Most agonistic activity was directed at other goldeneye brood hens (81%), but some (19%) involved Mallard (*Anas platyrhynchos*) and Wood Duck (*Aix sponsa*) brood

TABLE 3

PERCENT OF DIURNAL AGONISTIC TIME SPENT IN VARIOUS ACTIVITIES BY COMMON GOLDENEYE BROOD HENS IN MINNESOTA, 1984–1985

Activity	Interacting species	
	Goldeneye (N = 50)	Other[a] (N = 17)
Surface threat	66.7 (4.9)[b]	82.2 (8.7)
Shallow dive threat	23.7 (4.3)	12.4 (6.6)
Fighting	9.6 (3.4)	5.4 (3.4)

[a] Mallard and Wood Duck
[b] Mean (SE).

TABLE 4

PERCENT OF DIURNAL TIME SPENT IN PARENTAL CARE OR SELF-MAINTENANCE ACTIVITIES BY COMMON GOLDENEYE BROOD HENS IN MINNESOTA, 1984–1985

Activity	Island Lake (N = 78 h)	Lake Bemidji (N = 54 h)
Parental care	52.4 (2.1)[a]	45.8 (2.2)
Self-maintenance	47.6 (2.1)	54.2 (2.2)

[a] Mean (SE)

hens. However, type of agonistic activity was influenced by whether or not another goldeneye brood hen was involved (Table 3). Above water threats were more common when Mallard and Wood Duck hens were involved ($F = 5.36$; df = 1, 65; $P = 0.024$), whereas more intense dive threats and actual fighting were more prevalent when the interactions involved another goldeneye hen.

The proportion of time devoted to parental-care and self-maintenance behaviors was affected by location ($F = 5.15$; df = 1, 127; $P = 0.025$ and $F = 4.75$; df = 1, 127; $P = 0.031$) but not by year, brood age, or brood size (all P values > 0.11). Brood hens on Island Lake spent more time in parental-care activities and less time in self-maintenance than those on Lake Bemidji (Table 4).

Discussion.—Common Goldeneye hens divided their time nearly equally between parental care and self-maintenance. In contrast, Northern Pintail (*Anas acuta*) and Lesser Scaup (*Aythya affinis*) hens spent twice as much time in self-maintenance as they did in parental care (Rushforth Guinn and Batt 1985, Afton 1983). Likewise, activities that we considered self-maintenance also comprised about two-thirds of the time budgets recorded for Black Duck (*Anas rubripes*) and White-winged Scoter (*Melanitta fusca*) brood hens (Hickey and Titman 1983, Brown and Fredrickson 1987). Foraging generally is the largest fraction of self-maintenance and, except for scaup, time spent foraging by other species (35–50%) appears to be twice that of Common Goldeneyes. Foraging time was comparable to that of Lesser Scaup (Afton 1983) and Barrow's Goldeneyes (*Bucephala islandica*) (Savard 1988), and averaged 185 min/day on Island Lake and 255 min/day on Lake Bemidji. In comparison, goldeneye females on a nearby lake spent substantially less diurnal time foraging during egg laying but comparable time foraging during incubation (Zicus and Hennes 1993). Alert behavior was the major component of parental care, and goldeneye hens spent more time alert than species using less open habitat (see review in Afton and Paulus 1992).

We detected no brood-age or brood-size effects on parental investment by Common Goldeneye hens. Although these effects have been noted in other species (Morehouse and Brewer 1968, Johnson and Best 1982, and others), most studies have concerned species with altricial young. Factors influencing parental investment have been examined for some waterfowl (e.g., Afton 1983, Rushforth Guinn and Batt 1985, Lazarus and Inglis 1978), and hens of some species accompanying young broods have been reported to spend more time alert than when with older broods. However, the results have been equivocal (see review in Afton and Paulus 1992); perhaps, in part, due to difficulties in measuring alert behavior or that portion of it that is attributable to parental investment. Whereas we detected no brood-age effects on alert time, goldeneye hens spent more time pausing between foraging dives (and presumably alert) when with younger ducklings. In many studies, pauses between foraging dives have been considered foraging activity (e.g., Tome 1991, but see Brown and Fredrickson 1987). Because few relationships between brood size and parental investment have

been detected, Afton and Paulus (1992) concluded that parental investment in waterfowl is largely unshared (sensu Lazarus and Inglis 1986). Although total time in parental care was unrelated to brood size, goldeneye females with larger broods moved more as the brood foraged and spent less time in comfort activities than those with smaller broods. Females appeared to move more to remain vigilant over individual ducklings that were foraging somewhat independently of their broodmates.

Of the effects we examined, only lake had a significant influence on the division of diurnal time between parental care and self-maintenance. Most previous studies have not considered the effects that different locations or years might have on brood hen time-budgets. Influences of location or year on time allocation may be large relative to effects from such factors as brood age or size, thus making them easier to detect. Island Lake brood hens foraged, on average, 70 min/day less and spent 92 min/day more time alert than those on Lake Bemidji. Furthermore, although we detected no statistical difference, hens with broods tended to move more ($\bar{x}$ = 50 min/day) on Lake Bemidji than on Island Lake. Hunter et al. (1984) observed that Black Duck and Mallard ducklings spent more time moving and searching for food after invertebrate numbers were experimentally reduced. They also speculated that greater movement and other activities associated with increased foraging combined with decreased hen attentiveness might lower duckling survival.

Brood-rearing conditions on Island Lake are likely better than those on Lake Bemidji. A shallower basin with more highly developed stands of vegetation as well as a greater MEI should provide a more productive and diverse environment for invertebrates important as food. Additionally, less recreational boating might allow hens and broods to forage with greater efficiency and spend more time alert. Despite these lake differences, our observations are consistent with conclusions by Eadie and Keast (1982) that sites supporting both goldeneyes and fish should tend towards high levels of food production and resource diversity. Lake Bemidji was a productive lake and had many goldeneye pairs and broods. We also know of overland movements to the lake by goldeneye broods (Zicus, unpubl. data). Still, a better understanding of the relationships among invertebrate productivity and diversity in wetlands, waterfowl parental investment, and ultimately hen and duckling survival is needed before questions regarding possible fish-waterfowl competition for invertebrates can be fully resolved.

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Homosexual copulations by male Tree Swallows.—Homosexual courtship behavior in non-human animals is well known (Ford and Beach 1980) and occurs in a wide variety of taxa. However, homosexual copulations, especially between males, are less well known. In birds, males mounting other males have been observed in the colonially breeding Cattle Egret (*Bubulcus ibis*) (Fujioka and Yamagishi 1981) and Common Murre (*Uria aalge*) (Birkhead et al. 1985, Hatchwell 1988). Neither Fujioka and Yamagishi (1981) nor Birkhead et al. (1985) and Hatchwell (1988) reported whether cloacal contact occurred during their observations of male-male mountings. Here we describe homosexual copulations by male Tree Swallows (*Tachycineta bicolor*) during which cloacal contacts occurred.

In 1993, we studied the social and ecological correlates of the copulation behavior of Tree Swallows that bred in some of the 100 wooden nest boxes mounted on metal poles erected in old fields on the Grand Valley State University campus in Allendale, Ottawa County, Michigan. Nest boxes were arranged in grids, and each nest box was at least 30 m from its nearest neighbor. This spacing was similar to that found in a Canadian population of Tree Swallows using natural cavities as nest sites (Robertson and Rendell 1990).

Swallows were captured using a variety of trapping methods. We identified the sex of captured swallows by noting the presence of a well developed brood patch in females or a cloacal protuberance in males. Each captured swallow was banded with a U.S. Fish & Wildlife Service band and given a unique color mark, using water-proof marking pens and acrylic paints to facilitate individual identification.

At 07:00 EDT on 2 June 1993 we captured, measured, weighed, and color-marked the breeding male from box 42 as he entered the nest box to deliver food to six-day-old nestlings. Because of banding activities, male 42 was released approximately 500 m from box 42 near box 87. Upon his release, male 42 flew directly toward his nest box. As he passed in front of box 86 he was chased by several male swallows. He landed on the top of box 86 which was unoccupied. After male 42 landed, several male swallows attempted to copulate with him. It was clear that these were copulation attempts, because the males were hovering over male 42 and were making the "ticking" vocalizations characteristic of heterosexual copulations in Tree Swallows. At least one male achieved cloacal contact with male 42. After approximately 1 min, male 42 flew from box 86 to box 85, which was also unoccupied, where the males again hovered over his back and attempted to copulate with him. One male was perched on male 42's back for over 1 min and achieved cloacal contact more than once. All the while, the male held onto the feathers on the back of male 42's head and neck with his bill. Males commonly grab the backs of female necks and heads during heterosexual copulations in Tree Swallows. It was impossible to count the number of cloacal contacts because of the "cloud" of swallows fluttering around male 42. After several minutes perched on box 85, male 42 flew to box 84 followed by his pursuers. Box 84 was unoccupied as well. Male 42 landed on the top of box 84 and the events at boxes 86 and 85 were repeated. After approximately 1 min on top of box 84, male 42 disappeared in the direction of box 42, pursued by the group of male swallows.

There are several explanations for homosexual behavior in non-human animals. First, it is possible that the pursuers misidentified male 42 as a female because the plumage of after second year female Tree Swallows resembles that of males (Hussell 1983). Mistaken identity is a common explanation for homosexual mountings in insects (Thornhill and Alcock 1983). Both Birkhead et al. (1985) and Hatchwell (1988) concluded that homosexual mountings in the Common Murre were the result of mistaken identity; in their pursuit of extra-pair copulations, male Common Murres attempted to copulate with any individuals that returned to the breeding colony. Common Murres are sexually monomorphic. While mistaken identity

may explain why male 42 was pursued, it does not explain why he did not resist the copulation attempts and cloacal contact. Female Tree Swallows control copulation success (Lifjeld and Robertson 1992) and easily resist copulation attempts from extra-pair males and their mates alike by deflecting their tails preventing cloacal contact or by flying away (Venier et al. 1993; Lombardo, unpubl. data). We are positive that male 42 was a male for several reasons; it had a cloacal protuberance; it did not have a brood patch; its wing chord was 119 mm (Stutchbury and Robertson 1987); and the female at 42 had been marked previously and we had observed her incubating eggs. During observations during the nestling period, we observed male 42 assisting in the feeding of the nestlings in box 42 and defending the nest from our intrusions.

Second, homosexual behavior is sometimes seen in the context of reconciliation in primates (e.g., deWaal 1989). Reconciliation between prior antagonists is an unlikely explanation in this case because Tree Swallow sociality is not as complex as that of primates, and because the repeated interactions between individuals that favor reconciliation as a means of settling disputes are uncommon between distantly spaced breeding and relatively short-lived Tree Swallows (Butler 1988).

Third, expressions of dominance, subordinance, and appeasement are sometimes manifested as homosexual behavior (e.g., deWaal 1989). Interestingly, male Cattle Egrets that attempted homosexual copulations always ranked higher than, or equal to, the males that were targets of those attempts (Fujioka and Yamagishi 1981). This is a possible explanation for our observations, but it suggests a previously unimagined complexity of Tree Swallow sociality. However, it is of note that nests of the Cattle Egrets studied by Fujioka and Yamagishi (1981) were more closely spaced (average distance between nests of less than 2 m, Fujioka and Yamagishi 1981, Fig. 1) than those of Tree Swallows at our study site, thereby increasing the probability of establishment of dominance hierarchies between Cattle Egrets that have frequent interactions with each other. It is possible that male 42 may have avoided injury from his pursuers by displaying his subordinance to them by allowing them to copulate with him. Tree Swallows are capable of inflicting serious injuries on one another during fights (Lombardo 1986).

Fourth, Sauer (1972) hypothesized that homosexual behavior served as an outlet for sexual tension in South African Ostriches (*Struthio camelus*). This is an unlikely explanation for our observations, because we did not observe courtship displays, only chases, copulation attempts, and copulations.

Fifth, sexual play and experimentation are sometimes hypothesized as the explanation for homosexual behavior, especially by juveniles (Ford and Beach 1980). Sexual play and experimentation are unlikely as explanations for what we observed, because all of the males were sexually mature, and the interaction appeared aggressive rather than playful.

Møller (pers. comm.) has suggested that male birds may participate in homosexual copulations as a means of indirectly obtaining extra-pair copulations; sperm deposited by one male in the cloaca of another male could then be passed to the copulation partner of the latter when he copulates with a female. This explanation, while intriguing, is not completely satisfactory, because a stressed bird often defecates, voiding its cloaca of its contents. Male 42 defecated while we handled him, and he was undoubtedly stressed again by the onslaught of the males chasing attempting to copulate with him. We did not record whether he defecated during or after the sequence of events described above.

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Evidence of plural breeding by Red-cockaded Woodpeckers.—The endangered Red-cockaded Woodpecker (*Picoides borealis*) is a cooperatively breeding picid associated with mature pine forests of the southeastern United States (USFWS 1985, Walters 1990). Family groups typically consist of a monogamous breeding pair with one or more of their adult offspring serving as helpers (Ligon 1970, Lennartz et al. 1987, Walters et al. 1988). Helpers, which are almost exclusively male (Walters et al. 1988, Walters 1990), assist with incubation and feeding of nestlings (Lennartz and Harlow 1979). Breeding females typically produce a single clutch of 3–4 eggs (range 1–5) (Ligon 1970, Carter et al. 1983, Walters et al. 1988), although they will often renest if the eggs are lost to predation (Walters 1990). The nest usually is in the roost cavity of the breeding male (Ligon 1970, Walters et al. 1988).

We here report on some unusual nesting behavior exhibited by a group of Red-cockaded

Woodpeckers on Fort Bragg Military Installation in the Sandhills region of south-central North Carolina. During the 1993 breeding season, we observed one group that had two nests as well as an unrelated female helper. To our knowledge, plural nesting behavior has not previously been documented in Red-cockaded Woodpeckers. Immigrant females regularly attach themselves to groups as helpers or floaters (Walters et al. 1988, Walters 1990) but normally do not participate in breeding. The family group exhibiting the unusual behavior consisted of three banded birds: a seven-year-old male, a five-year-old female, and their two-year-old son. There also was an unbanded female of unknown age which we are confident was not related to any member of the group, as birds have been banded annually at this and adjacent sites since 1986. We captured and confirmed the sex of the unbanded female on 24 June.

The first nest, containing four eggs, was discovered on 3 May at 13:05 h during a routine nest survey. Prior to discovery of the nest, cavity trees were checked every seven days beginning 19 April. A bird flushed from the nest cavity on 26 April, but there were no eggs present at that time. We estimate the beginning laying date to be 27 April. This nest produced three nestlings. The second nest, containing three eggs, was discovered seven days after the first nest on 10 May in a lower cavity of the same tree. We presumed that this nest was being incubated, since a bird flushed from the cavity on 10 May at 12:15 h and on 13 May at 06:10 h. Later observations on 17 May and 20 May, however, revealed that incubation was no longer occurring, and the eggs in this nest never hatched. We suspected that the unbanded female produced the second clutch of eggs, because one female probably would not produce clutches of eggs in two cavities in such a short period of time. The cavity entrance of the second nest was slightly enlarged, but there were no other species of woodpeckers observed in the area during any of the observation periods. We did not retrieve the eggs, so we do not know whether the eggs were infertile or contained dead embryos.

In order to determine the role of the unbanded female in the family group, we made detailed observations of the birds on 17 May between 11:30 and 14:50 h. During this period, the nestlings were fed by all the birds in the group, although in disproportionate amounts. During the first hour, the nestlings were fed five times by the breeding female, four times by the unbanded female, three times by the helper male, and two times by the breeding male. There also were five times when we were unable to identify the bird feeding the nestlings. In addition, there was apparent conflict between the two females. For example, the breeding female blocked the cavity entrance for 20 min and aggressively deterred the unbanded female from feeding the nestlings.

The conflict between the two females did not cause the first nest to be unsuccessful. We banded three nestlings on 17 May. On 8 June, we observed that all three nestlings had successfully fledged (1M, 2F) and that the unbanded female was actively feeding all three fledglings, with no apparent conflicts between any of the adult birds.

We hypothesize that the unusual plural breeding behavior exhibited by the unbanded female may have occurred in response to limited breeding opportunities for young female Red-cockaded Woodpeckers on Fort Bragg. This observation supports Walters (1991) who reported that Red-cockaded Woodpeckers compete for breeding vacancies in existing groups, rather than form new groups. We also suggest that this type of adaptive breeding behavior may be how plural breeding originates in cooperative breeding systems.

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Wing-flashing in mockingbirds of the Galápagos Islands.—Wing-flashing is a conspicuous, stereotyped behavioral pattern of Northern Mockingbirds (*Mimus polyglottos*) that is used during foraging (Hailman 1960) and in the presence of potential predators (Hicks 1955, Selander and Hunter 1960). Its evolution and function are unclear, but study of the behavior among related species may suggest answers. In addition to the Northern Mockingbird, wing-flashing has been reported for the Gray Catbird (*Dumetella carolinensis*; Batts 1962, Michael 1970), Tropical Mockingbird (*M. gilvus*; Haverschmidt 1953, Whitaker 1957), Bahama Mockingbird (*M. gundlachii,* Aldridge 1984), Long-tailed Mockingbird (*M. longicaudatus,* Bowman and Carter 1971), Patagonian Mockingbird (*M. saturninus,* Halle 1948), the mockingbirds (*Nesominus* spp.) of the Galápagos Islands (Hundley 1963, Bowman and Carter 1971), Socorro Mockingbird (*Mimodes graysoni*; Curry and Martínez-Gómez, pers. comm.), and Brown Thrasher (*Toxostoma rufum*; Laskey in Sutton 1946, Tomkins 1950, Thomas in Whitaker 1957, Michael 1970). Unfortunately, these reports are often incomplete and frequently fail to mention the context in which the behavior occurred. We describe two incidents of wing-flashing in the Hood Island Mockingbird (*Nesominus macdonaldi*) of the Galápagos Islands.

On 23 May 1990 at 09:40 on Isla Genovesa (Hood Island) in the Galápagos Islands, Burtt, Porter, and Waterhouse noticed a snake (*Dromicus biserialis*) lying in an opening

between four *Cryptocarpus* bushes. The ground was hard and sparsely covered with short grass. The snake, which was about 60 cm long, was extended lengthwise in four loose curves. As we watched, an adult mockingbird ran toward the snake from under a bush to the snake's left. The mockingbird ran about 1 m and stopped about 25 cm to the left of the snake's head. When running, the mockingbird extended its wings horizontally with the primaries parallel to the body. The tail was held horizontally and was not fannned. When the mockingbird stopped, it folded its wings against its body, then suddenly and partially fanned them out from the body and up at a 45° angle. The motion lacked the brief hitch seen in the wing-flash of the Northern Mockingbird, and the hand remained folded so that the primaries remained parallel to the body. The tail was slightly raised and fanned 30° to the left and right of the center line. The wing-flash lasted less than a second. At no time did the bird crouch as if to fly. The mockingbird then hopped clockwise around the head of the snake to a point midway along the right side of the snake's body and about 12 cm away. The snake remained stationary. The mockingbird cocked its head to one side and then the other several times, always looking at the snake. During this examination its wings were folded against its sides. The snake now moved toward the bush to its right and the mockingbird hopped beside the snake. Just as the snake went under the bush the mockingbird delivered a peck toward its tail. We do not know if contact was made. After the peck the mockingbird turned 180° and hopped back to where the snake had lain, oriented toward the position the snake had occupied, and gave three wing-flashes in about 10 s before hopping to a nearby bush where it perched for several minutes.

On 19 May 1992 Swanson was studying displays of lava lizards (*Tropidurus delanonis*) on Isla Genovesa by presenting model lizards to resident individuals when a mockingbird approached a model, wing-flashed, and pecked the model. The mockingbird continued to wing-flash and attack for several minutes until Swanson removed her model and ended observations. On at least one wing-flash, the mockingbird raised its wings to about 80° above the horizontal, but in all other respects the behavior was exactly as described above. The lizard models were about 20 cm long.

These are the first descriptions of wing-flashing and its context in the Hood Island Mockingbird. Hundley (1963) described wing-flashing in the Chatham Mockingbird (*Nesomimus melanotis*), a brief comment by Curry (1986) suggests that the behavior occurs in the Galápagos Mockingbird (*N. parvulus*), and Bowman and Carter (1971) state that wing-flashing occurs in all four species of mockingbirds from the Galápagos Islands, but provide no descriptive or contextual details.

Given that wing-flashing occurs in at least eleven species of mimids belonging to five genera, the behavior would appear to be a primitive characteristic. Only one species, the Northern Mockingbird, has conspicuous markings that emphasize the wing motion, which suggests that the Northern Mockingbird's white wing patches evolved after the evolution of wing-flashing. However, unlike the Northern Mockingbird, which raises and fully extends its wings in a series of "hitches" (Hailman 1960), the Hood Island Mockingbird raises its wings in a single motion and the primaries remain folded. Similarly, Hundley (1963) observed that wing-flashing in the Chatham Mockingbird ". . . lacked somewhat the 'one-two-three,' drill-like precision of our northern species . . ." and that the wings were raised only slightly above the horizontal. Thus the action pattern of the Northern Mockingbird with its full extension of the wing and its "hitches" appears more exaggerated and more mechanical than the displays of mockingbirds that lack conspicuous white wing patches, for example the Hood Island Mockingbird. We conclude that the wing motion evolved first, that the white patches, which dramatize the motion, evolved secondarily, and that the patches selected for evolutionary exaggeration of the wing motion. Such positive feedback between behavior and color pattern occurs in the wood-warblers where aerial displays occur in many

species, but wingbars and tailspots are associated with the most dramatic aerial displays (Burtt 1986). White wing patches may have evolved in mockingbirds to emphasize the wing motion of other action patterns (e.g., jump-song). Nonetheless, the evolution of conspicuous patches would select for exaggerated wing-flashing, whether the behavior functioned to signal conspecifics or startle prey (Hailman 1960).

The function of wing-flashing is unclear, but its context appears consistent across species. In the Northern Mockingbird wing-flashing occurs when birds encounter strange objects or unexpected movements or noises (Horwich 1965). In these situations, which may occur when confronting prey (Hailman 1960) or a passive predator (Selander and Hunter 1960), the mockingbirds are wary but not completely frightened. When suddenly confronted with a snake, the Hood Island Mockingbird gave a wing-flash but gave no additional wing-flashes while the snake remained stationary. This is similar to a snake attack by the Northern Mockingbird (Hicks 1955), except for the three wing-flashes given by the Hood Island Mockingbird after the snake's disappearance. However, the incident observed by Hicks ended when he chased the snake away so we do not know what the Northern Mockingbird might have done after the snake's departure. Presentation of models to Northern Mockingbirds (Horwich 1965) elicited frequent and persistent wing-flashing as did presentation of Swanson's lizard models to the Hood Island Mockingbird. Thus the context of wing-flashing in the Hood Island Mockingbird appears to be similiar to the context of the more conspicuous, dramatic wing-flashing of the Northern Mockingbird.

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Tree nesting by Wild Turkeys on Ossabaw Island, Georgia.—In the spring of 1988, seven Wild Turkey (*Meleagris gallopavo*) poults were found either wandering or stunned near the base of a large live oak (*Quercus virginiana*) on Ossabaw Island. Ossabaw Island is a 10,117 ha barrier island consisting of approximately 4775 ha of uplands, with the remaining acreage consisting of salt marsh. A detailed description of plant communities of Ossabaw is given by Johnson et al. (an ecological survey of the coastal region of Georgia, U.S. Govt. Printing Office, 1974). The live oak had a diameter at breast height (dbh) of approximately 1.2 m. At about 2.4 m high several limbs originated, forming a large crotch covered with resurrection fern (*Polypodium polypodioides*). Examination of the tree crotch revealed a nest containing eggshells from hatched poults. Some poults had injuries from the fall, but most appeared to be in good health. During the spring of 1989, a Wild Turkey hen was observed incubating 11 eggs in the same tree. All 11 eggs hatched. The hen was observed at the base of the tree calling to the poults. Three poults jumped out of the tree and followed the hen away from the nest. The remaining eight poults in the tree were abandoned. A Wild Turkey also was observed nesting in the same tree in 1990. Poults were not seen during or after hatching; however, eggshells from several turkey eggs were recovered from the nest during mid-July, 1990. The tree was not used during the 1991 nesting season. Evidence of a turkey nest in a second live oak also was found on Ossabaw Island during the summer of 1988. The tree had a dbh of 1.8 m and a crotch at about 1.5 m. Wild Turkey eggshells were found in the mat of fern in the tree crotch and at the base of the tree. Wild Turkey nesting was not detected in the tree during the 1989, 1990, or 1991 nesting seasons.

Although the Wild Turkey is a ground nester (Williams, The book of the Wild Turkey, Winchester Press 1981), above-ground nesting of two Wild Turkey hens in North Carolina was described by Cobb and Doerr (Wilson Bull. 101:644–645, 1989). Unlike Ossabaw, the nests were in old growth water tupelo (*Nyssa aquatica*)/bald cypress (*Taxodium distichum*) backswamp. Also, the North Carolina nests were on a log (65.5-cm tall) and a stump (1.4-m tall) compared to live trees on Ossabaw. Cobb and Doerr (1989) pointed out that above-ground nests they observed had the advantage of being above the normal field of view of ground predators. In addition, the nests were less likely to be destroyed by flooding.

Three hypotheses may explain tree nesting by Wild Turkeys on Ossabaw Island. Feral hogs (*Sus scrofa*) (>24.7/km^2) and raccoons (*Procyon lotor*) (>4.0/km^2) both occur on Ossabaw (Fletcher et al., J. Wildl. Dis. 26:502–510, 1990). Tree nesting may be an attempt to prevent nest depredation by these species. Additionally, high populations of deer and exotic browsers and grazers have greatly reduced understory nesting cover (Johnson et al. 1974), limiting suitable ground nesting sites. Last is the availability of trees large enough and with suitable configurations to accommodate a turkey nest. Few places exist where trees similar to the size and shape of the live oaks on Ossabaw are accessible to nesting Wild Turkeys.

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Post-hatch brood amalgamation by Black-bellied Whistling-Ducks.—Post-hatch brood amalgamation (post-HBA) occurs when parents incubate and hatch their own young, but subsequently rear young of other individuals as well. The term also applies to cases in which young are reared by other adults as well as situations in which pairs cooperatively rear their broods together (Eadie et al. 1988, Afton 1993). Afton and Paulus (1992) reported that brood amalgamations have been described in 41 waterfowl species. Eadie et al. (1988) and Afton and Paulus (1992) grouped post-HBA into four categories: (1) *adoption,* a pair or single female accepting foster young into their own brood, (2) *creche* or *mixed brood,* a group of birds containing any number of adults (not necessarily related to the young) plus two or more young which are parentally unrelated, (3) *gang-brooding,* mated pairs or several different females with their associated broods joining together, and (4) *kidnapping,* a pair or dominate female which aggressively kidnaps young of a subordinate pair or female. However, no records of post-HBA in the tribe Dendrocygnini have been recorded (Afton and Paulus 1992). I report here the first occurrence of post-HBA in Black-bellied Whistling-Ducks (*Dendrocygna autumnalis*).

On 3 June 1987, I received 30 one-day-old Black-bellied Whistling-Duck ducklings obtained from a single nest by personnel of the Texas Dept. of Parks and Wildlife. Six ducklings died within the first 3 h of captivity. The ducklings were housed at the Caesar Kleberg Wildlife Research Institute's South Pasture Facility 10 km south of Kingsville, Texas. They were fed a mixture of chick starter and water ad libitum and were housed for two weeks in a brooder. Subsequently they were moved to a pen that was half indoors and half outdoors (4 m length × 2 m width × 2 m height). The outdoor half of the pen was enclosed with 2.54 cm chicken wire and an electric fence to prevent predation. Four ducklings escaped the outdoor pen through the chicken wire fence. The outdoor pen also contained a 151-L water tank for the birds.

During the growth and development of these ducklings, adult whistling-ducks regularly visited the pen. During the first 2 h of daylight, adults perched on top of 2.5-m fence poles leading out from the duckling housing facility. The adults vocalized, and the ducklings responded, presumably in response to the adult calls. After perching on the fence posts, the adult Black-bellied Whistling-Ducks would then fly to a 4-ha pond 300 m north of the duckling pen. The peak number of adults on the fence posts in the morning was 28. On at least five occasions, one pair of adults would perch on individual 2.5-m poles next to the duckling pen and stay throughout the day. When the adults were leaving the pond in the evening, up to eight would perch on the poles and vocalize. Vocalizations by adults and ducklings would occur while they were in visual proximity of one another and continue until 0.5 h of light remained in the day at which time the adults would leave toward the south.

The remaining 20 ducklings made their first attempt at flight on 8 July 1987 and were

subsequently released on the pond. The young birds swam to the middle of the pond, responding to the calls of the adults. The released ducklings were joined by four families from the surrounding brush and water edge. Each family consisted of two adults and consisted of five, seven, four, and three ducklings, respectively. The four naturally occurring and the one released broods amalgamated with two adults from one of the families. I assumed the adults to be a male and a female because previous research has shown that adults of both sexes tend to their young equally (Bolen 1971, 1979; McCamant and Bolen 1977; Rylander et al. 1980). The other adults joined the flock of Black-bellied Whistling-Ducks using the pond. Approximately 90 adult Black-bellied Whistling-Ducks spent each day on the 4-ha pond north of the ducklings' pen. The adults used the surrounding brush, trees, and water edges. The post-HBA was checked at least twice daily, 4 h after sunrise and 4 h before sunset, and when other time periods permitted. Observations of the brood lasted from 10–30 min. The post-HBA spent its time near the edges of the pond moving to the middle of the pond when there was potential danger. The adults not with the brood continued to return to and leave from the pond each day. A pair of adults and the brood remained intact for four weeks. At the end of the four weeks on the pond, the adults and brood joined up with the flock of Black-bellied Whistling-Ducks using the pond and began to participate in the daily movements.

My observation is the first post-HBA reported for Black-bellied Whistling-Ducks. The post-HBA is a combination of Eadie et al. (1988) and Afton and Paulus' (1992) category 2 of creche or mixed brood and category 1 for adoption. Additional observations are needed to determine the factors influencing post-HBA in Black-bellied Whistling-Ducks.

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Sharp-shinned Hawk preys on a Marbled Murrelet nesting in old-growth forest.— Few details of the life history of the Marbled Murrelet (*Brachyramphus marmoratus*) are known. However, it appears that murrelets do not breed until about three years old, lay only one egg, and, like other alcids, are probably long-lived (Sealy 1974a, 1975; Evans and Nettleship 1985). Marbled Murrelets are unusual among the Alcidae because they nest primarily in old-growth coniferous trees, where the adult's mottled red-brown plumage camouflages it in moss- and lichen-covered branches (Binford et al. 1975, Quinlan and Hughes 1990, Singer et al. 1991). Murrelets exchange incubation duties and feed chicks most frequently during the low light levels of dawn. They typically are silent when approaching and departing from nests (Singer et al. 1991, Naslund 1993). After leaving the nest, murrelets sometimes erratically fly at rapid speed through the forest (unpubl. obs.). The cryptic coloration, secretive behavior and possibly predator-confusing flight pattern, suggests that predation pressures are important at murrelet nests.

Raptor predation on adult murrelets appears to occur with some regularity in coastal areas. Predators have included Peregrine Falcons (*Falco peregrinus*), Bald Eagles (*Haliaeetus leucocephalus*), and possibly Merlins (*F. columbarius*; Sealy 1975; Quinlan and Hughes 1992; J. Hughes, pers. comm.; L. Prestash and R. Burns, pers. comm.). Predation on Marbled Murrelet eggs and chicks has also been documented and may account for a large percentage of nest failures throughout the murrelets' range (Singer et al. 1991, Nelson and Hamer 1992). It appears that corvids are the major predators at murrelet nests. In California, a Steller's Jay (*Cyanocitta stelleri*) took a young murrelet chick from an unattended nest, and an embryo or part of an adult murrelet was carried away from a murrelet nest by a Common Raven (*Corvus corax*; Singer et al. 1991, Naslund 1993). In the Pacific Northwest, a Great Horned Owl (*Bubo virginianus*) preyed on a Marbled Murrelet nestling, and predation was found to be the primary cause of nesting failure (Nelson 1991, Nelson and Hamer 1992). Here we describe predation of an adult Marbled Murrelet at its nest in old-growth forest by a Sharp-shinned Hawk (*Accipiter striatus*).

While conducting dawn surveys of Marbled Murrelet habitat (see Paton et al. 1990) throughout Naked, Peak, and Storey islands in Prince William Sound, Alaska, we recorded all murrelets seen or heard during a 2-h period beginning 90–105 min prior to official sunrise. One survey, approximately 180 m from the ocean and 120 m in elevation, was conducted on Storey Island. The dense stand of western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), and mountain hemlock (*T. mertensiana*) at this site included trees more than a meter in diameter at breast height (dbh). Trees in this stand were among the largest observed on this group of islands (for the largest 20% of trees >10 cm dbh in a 25 m radius plot, $\bar{x}$ = 83 cm dbh; Kuletz et al., unpubl. data). Canopy closure was approximately 85%, and there was a sparse understory of blueberry (*Vaccinium alaskensis*), rusty menziesia (*Menziesia ferruginea*), salmonberry (*Rubis spectabilis*), a variety of ferns, and thick moss on the trees and ground. Large moss-covered platforms were common on trees more than 70 cm dbh.

At 04:33 h ADT (38 min before official sunrise) on 11 July 1991, DKM heard a sharp keer call and the characteristic wingbeat sound of a murrelet landing in a tree about 40 m away. About 5 sec later, murrelet wingbeats were heard moving away from the tree, heading toward the ocean. After approximately one min, a Sharp-shinned Hawk called, followed immediately by another sharp keer call and murrelet wingbeats. At 04:44 h (still twilight and 27 min before sunrise), loud wing sounds revealed a murrelet again flying into the tree. It immediately flew out and for 3–5 sec the loud flapping of its wings could be heard descending slowly toward the ground. After 15 min, at the survey's conclusion, a Sharp-

shinned Hawk was observed on the ground in the vicinity of earlier activity and was flushed from a Marbled Murrelet. The dead murrelet was a 200-g adult male with an empty stomach and a large (35 × 20 mm) vascularized brood patch. The size of the brood patch indicated current or recent incubation (see Sealy 1974b). A 3-cm patch of breast feathers had been plucked by the hawk. Based on size and plumage, the Sharp-shinned Hawk was an adult female, which probably belonged to a pair observed in the same area during the previous afternoon. Three upper canopy trees in the vicinity were climbed, but no murrelet nest was found.

Sharp-shinned Hawks prefer large nest trees that provide cover and physical protection from predators (Clarke 1982, Reynolds et al. 1982). Therefore, it was not unusual to find them nesting in proximity to Marbled Murrelets. However, the murrelet was among the largest prey taken by a Sharp-shinned Hawk (McAtee 1935) and probably matched or exceeded the weight of the hawk (range of female Sharp-shinned Hawk masses: 120–210 g; Palmer 1988).

This is the first confirmed account of predation on an adult Marbled Murrelet at its nest. Compared to predation on eggs or nestlings, the loss of breeding adults may have a greater impact on the population of this potentially long-lived and slow-reproducing species. Along with breeding experience, nest site quality is probably critical to breeding success. Predation may be a major factor in determining the quality of a nest site. Vegetation and habitat characteristics (e.g., cover provided by surrounding foliage, ease of accessibility, stand size, light levels, and other factors influencing bird visibility) may increase the quality of a nest site by reducing susceptibility to predation. Our observation documents that adult murrelets are vulnerable to predation at nests and helps to explain the murrelet's cryptic plumage and secretive behavior at nest sites. Predation has been implicated in the evolution of nocturnal and crepuscular activity patterns for other nesting alcids (McNeil et al. 1993). Similarly, Marbled Murrelets may visit inland nesting areas primarily during the low light levels of dawn and dusk to minimize threats from diurnal predators.

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Use of bait and lures by Green-backed Herons in Amazonian Peru.—Use of bait and lures by Green-backed Herons (*Butorides striatus*) has been documented in Africa (Boswall 1983, Walsh et al. 1985), the southeastern United States (Lovell 1958, Sisson 1974, Keenan 1981, Preston et al. 1986, Higuchi 1988a), Cuba (Boswall 1983), and Japan (Higuchi 1986, 1988b). Green-backed Herons have been observed using both lures (e.g., feathers, fruit, flowers) and potential food items (e.g., insects and crackers) as bait to attract fish (reviewed in Higuchi 1986). Sisson (1974) photographically documented the use of bait in Florida. The use of bait and lures is an apparent case of true tool use (Higuchi 1986, 1988b). In this note, I document the use of bait and lures by Green-backed Herons at a site in the western Amazon basin of Peru.

The observations reported here were made in the vicinity of the Cocha Cashu Biological Station in the lowland (300–350 m) section of the Manu National Park of southeastern Peru (11°55′S, 77°18′W). Cocha Cashu is an oxbow lake of the Manu River in an extensive area of undisturbed floodplain forest (see Bolster and Robinson 1990 for a description and map of the study area). All observations of bait fishing occurred during an eight-day period, 3–10 November 1988. Observations were made from boats through 10× binoculars. The first bird observed using bait was photographed using a 500-mm lens (photographs available upon request from the author). On 10 November 1988, I paddled the canoe slowly around the margins of the lake in an effort to determine how many individuals were using lures

and baits. I repeated this process five more times in September, 1989, to search for possible bait fishing. Willard (1985) presented data on foraging of Green-backed Herons in the same oxbow lake, 1975–1976, although none was observed using bait (see below). Two of the individual Green-backed Herons observed using bait and lures were individually color banded.

The first observation of the possible use of lures was on 3 November 1988 when an unmarked adult was observed foraging on exposed branches of a fallen tree 10–15 m from the edge of the lake. The heron was first observed at 16:54 when it was holding a small (ca 1 cm diameter) round winged seed in its bill roughly 20 cm above the water. The heron picked up and dropped the seed in the water 27 times during the next five minutes after which it caught a small fish of approximately 4 cm. Each time the heron dropped the seed at least 10–15 cm above the water. The heron adopted a crouched position and pointed its bill and neck at the seed each time it dropped it in the water. After catching the fish, the heron flew approximately 10 m to a new perch roughly 15 cm above the water and picked up a small (<1 cm) pink flower and dropped it in the water six times, using the same postures it used with the seed. After three min of using the flower, it switched to a small green leaf fragment. During the next nine minutes, it used two more leaf fragments and a twig, after which it flew into dense lake-margin vines where I lost sight of it. During 18 total min of foraging (including one min to handle the fish), the heron caught one fish using five different bait items.

During a census of the entire lake on the afternoon (14:30–17:30) of 10 November 1988, I observed Green-backed Herons foraging seven times. Four of these observations were of herons using bait and/or lures, whereas the other three did not involve the use of bait during 3–10 min observation periods. Two of the individuals using bait were individually marked; therefore, at least three individuals used bait. One observation was of a bird twice dropping a small (ca 2 cm) twig into the water, another dropped a small (1–2 cm) unidentified object at least twice, and the third dropped a small (one cm) white flower into the water three times. None caught a fish. The individual that used a twig obtained it by breaking it off a hanging branch approximately 40 cm above the water after which it flew about two m and began to drop it in the water. The fourth record was of a color-marked individual that placed a living tabanid fly (ca 1.5 cm) four times in the water. The fly swam around in circles as the heron watched. During a period of approximately five minutes, the heron failed to catch a fish and carried the fly to a new perch.

In 1989, I conducted four censuses of Cocha Cashu during September and failed to observe a single case of bait fishing among 39 observations (at least one min of hunting each) of at least eight individual Green-backed Herons. During the previous nine field seasons, I had never noticed bait fishing in Green-backed Herons, although I was not studying them. Willard (1985) also observed no bait fishing in Green-backed Herons during his study of fish-eating birds on Cocha Cashu, 1975–1976. These observations support Higuchi's (1988a) suggestion that bait fishing may be sporadic in time and place.

These observations appear to be the first documented case of the use of bait by Green-backed Herons in South America. There are now records from Asia, Africa, North and South America, and the West Indies (reviewed in Higuchi 1986). Bait fishing in Amazonian Peru was similar to that reported in Japan (Higuchi 1988b) where the herons also used objects that were floating on the lake surface and were broken from dead branches. The use of the live tabanid was similar to the use of mayflies (Ephemeroptera) in North America (Keenan 1981, Preston et al. 1986). There were no man-made objects floating in Cocha Cashu; for this reason, all objects were natural. I could not determine if the objects were being used to attract particular fish or if they waited for any fish to approach the bait. The water of Cocha Cashu is murky with poor visibility; it is therefore possible that the herons

were not baiting particular fish as they do in Japan (Higuchi 1988a, b). The individual that broke a small twig from a dead fallen branch manipulated a substrate, possibly to make a piece of a lure.

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Carolina Chickadee lays and incubates eggs in two separate nest cups within the same nest box.—From 22 April until 10 June 1993, we observed an unusual Carolina Chickadee (*Parus carolinensis*) breeding attempt in a cedar nest box located directly under a 765,000-volt transmission line in Alum Creek State Park, Delaware County, Ohio (40°11′5″N 82°57′20″W). On 2 May, there were two eggs in a nest cup constructed on one side of the nest chamber. Over the next three days, three additional eggs were laid in a separate cup located on the other side of the box (Fig. 1A). On 9 May, we caught and banded a female chickadee as she incubated two eggs in the first nest cup. On 16 May we caught the same chickadee as she incubated a set of three eggs in the second nest cup. All

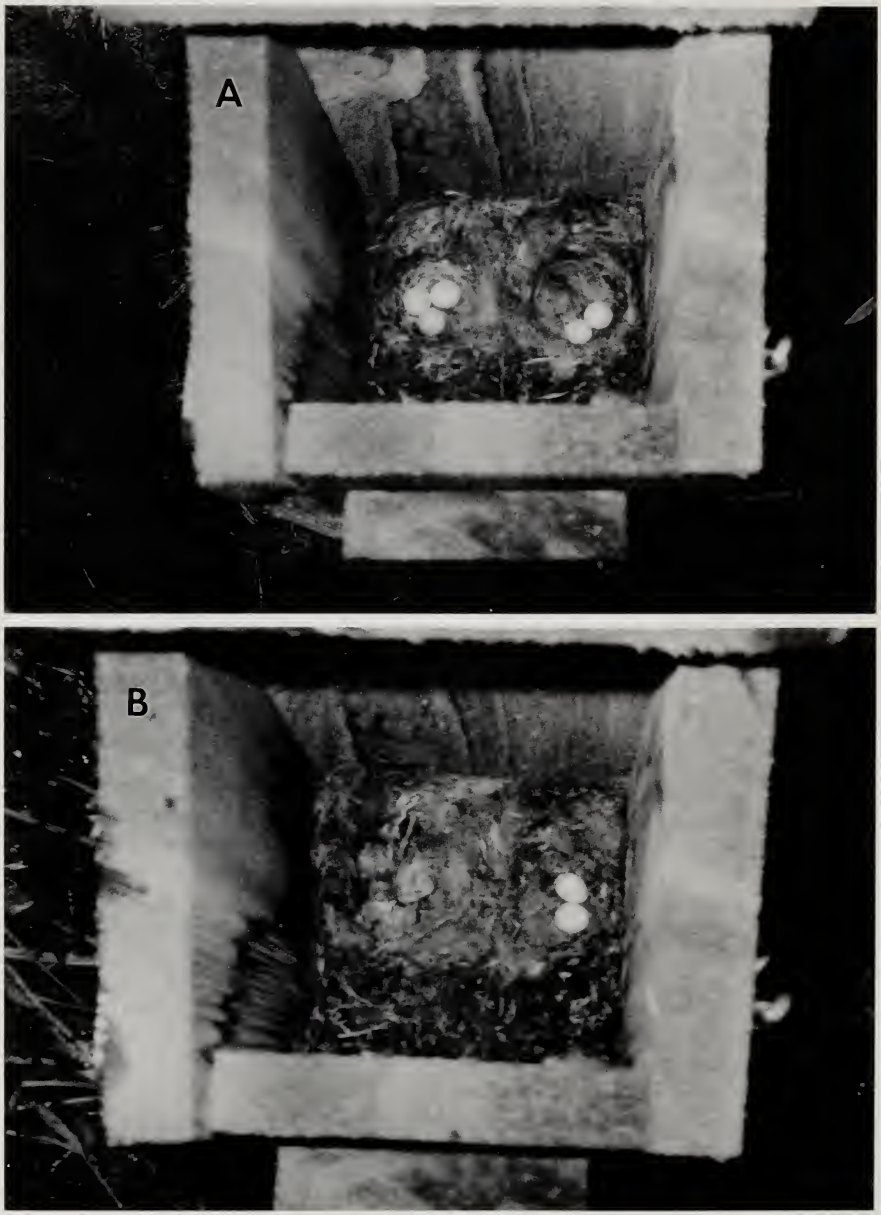

FIG. 1. (A) Two Carolina Chickadee nest cups within the same nest box. (B) Three nestlings in one nest cup, one of which survived to fledging. Neither egg in the other nest cup hatched.

five eggs were warm to the touch throughout the incubation period, an interval during which the box was checked at least every second day. On 18 May, the set of three eggs hatched (Fig. 1B). The set of two eggs never hatched and eventually disappeared on 31 May. Two of the three nestlings disappeared, one six days after hatching, and the other 13 days after hatching. The third fledged 18 days posthatch. A sixth chickadee egg was laid in the nest containing the lone nestling on 2 June, three days before the surviving nestling fledged. This egg disappeared when a House Wren (*Troglodytes aedon*) took over the box on 10 June.

Although Gowaty (Wilson Bull. 95:148–150, 1983) has found two Eastern Bluebirds (*Sialia sialis*) occupying the same nest box, apparently such was not the case here for chickadees. We believe that the same bird laid the aggregate of five eggs in two nest cups because the eggs were laid sequentially, one per day, over a five day period and because the same bird was caught incubating both sets of eggs. Also, except for the female's apparent mate, we never observed any other chickadee around the box.

As the nest box was located directly under the high-voltage line, it is problematical whether the electromagnetic field influenced the bird. During the same breeding season, two other chickadee nests under the powerline were successful (≥ one fledgling) and three nests failed. In a control area nearby, but beyond the powerline's electromagnetic field, no Carolina Chickadee nests were successful and two nests failed. However, only in the one "experimental" nest was the behavior of a female apparently aberrant.

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When is the Common Raven Black?—Adults of the genus *Corvus* typically have plumage similar to that of juveniles, but Wilmore (1977), Coombs (1978) and Goodwin (1986) all state that juvenile Common Ravens (*C. corax*) have "duller" plumage than adults. Kerttu (1973) also describes juveniles as having dull plumage, with only second-year birds acquiring the shiny metallic sheen of adults. However, Witherby et al. (1943) state that in the juveniles the "tail, wings and wing-coverts are much as in the adult, but not so brightly glossed," and then mention that the gloss becomes "almost entirely worn off by the first autumn." Bent (1946) reports that the wings and the tail of juveniles are "much like those of the adult, clear lustrous black with greenish and purplish reflections" and, that at the end of the juvenile molt completed in late summer, "the winter plumage is practically adult, lustrous black." These three conflicting claims could lead to confusion in age determinations so critical in unravelling the social behavior of many corvids (for example, Henderson and Hart 1991).

To distinguish juvenile from adult ravens, Kerttu (1973) delineated three age classes based primarily on palate color. However, palate color is a plastic characteristic in ravens, highly dependent on status and possibly mate-bonding (Heinrich and Marzluff 1992), making it an unreliable indicator of age beyond the first summer. This leaves plumage characteristics as

a possible aging tool, but only if the three conflicting claims regarding juvenile plumage can be resolved.

In *Corvus* the first molt occurs in the summer or early fall and involves the replacement of dull-colored juvenal body plumage and wing coverts with glossy basic feathers. Juvenal remiges and rectrices, however, are not molted until the following summer (Bent 1946) and then only over a relatively long time so that flight ability is not compromised (Gwinner 1966).

To resolve the apparent discrepancies of whether juveniles have dull or shiny feathers, I photographed ravens of various known ages. Observations are based on ten birds hand-reared from nestlings, and 14 wild-captured birds maintained for at least one year in an outdoor aviary, and birds in the wild.

Like Bent (1946), I found that the juvenal body plumage of ravens is dull-colored and that the young lack lanceolate throat hackles. Nevertheless, although the juvenal body plumage is dull-colored, the remiges, retrices, and wing coverts of nestlings are sleek and shiny with bluish, green, and olive sheen, almost indistinguishable from those of adults. By late July the shiny adult-like contour feathers appear as well, including the long lanceolate throat feathers typical of the adults. In addition, the dark sheen of the remiges and retrices remains until at least six months post-fledging. Thus, by late summer or early fall, when the young disperse, they have virtually adult plumage. A few months later, however, they can again be distinguished from adults by their plumage. Photographs are available from VIREO.

All of the 14 wild-caught ravens that had brownish remiges and retrices in February of the first winter had glossy adult-like remiges and retrices the following February. I conclude that the shiny juvenal tail and wing feathers fade to a dull brown over the first winter and that birds aged one or more years remain dark and glossy.

After the first year, a complete prebasic molt occurs every summer, and the second and subsequent sets of wing and tail feathers thus show little or no loss of sheen throughout the year. In summary, these results are in partial agreement with all of the authors cited, but they are not in full agreement with any of them.

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Feeder access: deceptive use of alarm calls by a White-breasted Nuthatch.—While observing interactions among birds visiting my feeder, I noticed several instances of apparent deceptive use of alarm calls by one or more White-breasted Nuthatches (*Sitta carolinensis*). The observations were made at a six-perch oil seed feeder at my home in Waterville, Lucas County, Ohio, during the winters of 1989–1990 through 1991–1992.

In each instance, a nuthatch approached the feeder while it was occupied by three to six other birds, usually House Finches (*Carpodacus mexicanus*). The nuthatch perched 6–10 m from the feeder, either in the overhanging branches of a black walnut (*Juglans nigra*) tree or clinging to the brick wall of our house. After watching the activity at the feeder for a few seconds, the nuthatch uttered a loud, rapid series of high-pitched "yank-yank" notes, seemingly identical to the alarm calls given by nuthatches when Cooper's (*Accipiter cooperii*) or Sharp-shinned (*A. striatus*) hawks appear in our yard. Upon hearing the call, birds at the feeder flew immediately to cover in nearby shrubbery. Simultaneously, the nuthatch flew directly to the feeder and began extracting seeds.

Accipitrine hawks are frequent visitors to our yard, so birds at the feeder apparently receive enough positive reinforcement to continue to respond to all alarm calls as if an accipiter were present. Although two or more nuthatches reside almost continuously within sight of the feeder each winter, I have observed the deceptive use of alarm calls by nuthatches infrequently—perhaps eight times in more than 50 h of feeder watching. Most often, a nuthatch would simply fly directly to the feeder and displace a House Finch from one of the perches by probing at it with its bill. But deceptive alarm calling allows a nuthatch to gain feeder access without risking injury in a physical encounter with another bird. Perhaps, like the boy who cried "wolf," a nuthatch who uses the deceptive alarm call strategy too often might eventually render it ineffective. It would be interesting to know what special circumstances, if any, cause nuthatches to choose this strategy.

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Unusual copulatory behavior by Fiery-throated Hummingbirds.—On 17 June 1991, we discovered two Fiery-throated Hummingbirds (*Panterpe insignis*) lying together on the ground in the middle of a foot path at 2650 m elevation in Parque Nacional Volcan Poas, Alajuela Province, Costa Rica. The two birds appeared to be copulating; their cloacas were joined, and one bird clung tightly with its feet to the feathers of the other's lower back and made occasional thrusting motions with its abdomen. The habitat was an epiphyte-laden elfin forest with abundant leaf litter on the ground. Dominant large plants included *Clusia* and *Gunnera* species. During about 15 min of observation, the putative female (the sexes are similar in this species) attempted several times to disengage and fly off, but the mounted (male?) bird kept its grip on its partner's back and remained firmly attached. During these attempts to disengage, the two birds spun wildly about on the ground with the female (?) giving a series of rapid, buzzy scolding notes. Simmers returned to the spot 35 min later and found the birds still in a copulatory position in the middle of the trail. After a few more minutes they finally separated and flew off in different directions. As they separated a drop of clear fluid (semen?) was shed from the rear of the female (?) bird, presumably from the

cloacal opening. This behavior is unusual in two respects: (1) The long time of coupling. The birds were already copulating when we discovered them and, therefore, were together for over 50 min and possibly for much longer. (2) The unusual location on the leaf litter of the forest floor rather than on a branch. We are unaware of any records of copulation on the ground or for prolonged intervals by hummingbirds. It seems doubtful that such behavior is adaptive, given the extreme vulnerability of the birds to predators while so engaged.

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First description of the nest and eggs of the Sooty-faced Finch.—Sooty-faced Finches (*Lysurus crassirostris*) occur in dense undergrowth of wet forests that border streams along the Caribbean slope of Costa Rica between 600 to 1500 m in altitude. Its distribution is from Cordillera de Tilarán in Costa Rica to eastern Panama (Slud, *The birds of Costa Rica. Distribution and ecology.* Bull. Amer. Mus. of Nat. Hist. 128, 1964; Stiles and Skutch, *A guide to the birds of Costa Rica.* Cornell Univ. Press, Ithaca, New York, 1989).

On 5 May, 1993, I found a Sooty-faced Finch nest containing two eggs at the Reserva de San Ramón on the Caribbean slope of Costa Rica (800 m; 10°13′N and 84°37′W). The nest was attached to a fern stem 1.5 m above the ground in primary forest. The nest was roofed and had a side entrance, the 15 × 13 cm cavity was lined with fern rootlets and bamboo leaves. A soft bulk of moss decorated with fern leaves and *Selaginella* surrounded the outer part of the cavity and extended, just touching the fern trunk, for 67 cm below the nest. The nest contained two short-oval shaped eggs (terminology of Harrison, *A field guide to nests, eggs and nestlings of North American birds.* Collins, Toronto, Ontario, 1984) with the following dimensions and mass, respectively: 24.85 × 18.90 mm and 25.00 × 18.75 mm; and 4.5 and 4.6 g. The eggs were ivory-colored with vinaceous-pink spots (Smithe, *Naturalist's color guide.* Amer. Mus. Nat. Hist. New York, New York, 1975) covering most of the wide tip and dispersed speckles (of the same color) toward the narrow end. Embryonic development had just begun in one egg but not in the second. This is the first description of the nest and eggs of this species. The nest and eggs were deposited in the ornithology collection of the Museo Nacional de Costa Rica.

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ORNITHOLOGICAL LITERATURE

HANDBOOK OF THE BIRDS OF THE WORLD. VOLUME 1: OSTRICH TO DUCKS. By Josep del Hoyo, Andrew Elliott, and Jordi Sargatal (eds.). Lynx Edicions, Barcelona, Spain. 1992:696 pp., numerous color photographs, maps, and illustrations. $165.00.—The present volume is the first of a series that review the birds of the world in a progressive, phylogenetic fashion. After an introduction describing the general organization and purpose of the work, the book discusses the general anatomy, natural history, evolution, and taxonomy of the Class Aves. The remainder of the book is divided into sections progressively dealing with orders of birds from ostriches through ducks, geese, and swans. The discussion of each order begins with a general review of the group. Each section ends with a review of the species in the order, providing detailed taxonomy, a map of each species' distribution, and numerous references to the scientific literature dealing with that species. Final sections include references to the original scientific descriptions of each species and a fairly lengthy list of references.

This book is large in size, scope, and price, but in my view all are justified. The book should contribute to the education of persons interested in birds, but who do not possess an extensive library dealing with avian biology, taxonomy, and distribution. I applaud the combination of readable prose, extensive use of the scientific literature and beautiful, high-quality illustrative materials. The result is a very attractive volume. The text does not appear to be directed to the casual reader or the professional, but may reach an audience that often is ignored—the scholarly nonprofessional.

The book could have benefitted from some close editing. There are numerous variations of format, style, and English usage that detract somewhat from the overall appearance of the volume. An errata sheet has been issued with "sticky" corrections that may be detached and inserted into the book. My copy of the book had a few poorly printed pages on which it appeared that the press was not fully inked.

In summary, this book may well be a useful adornment to our coffee tables or may provide useful summaries of birds with which we are not familiar, but it will not replace good field guides, checklists, and more scientific texts.—C. R. BLEM.

AVIAN SYSTEMATICS AND TAXONOMY. Bulletin of the British Ornithologists' Club Centenary Volume, Supplement 112A:1–309, The British Ornithologists' Club, Henry Ling Ltd., Dorset Press, Dorchester, Dorset. Price not given—In his interesting chapter on estimating the direction and strength of natural selection, Peter Grant noted that modern systematic biology has been revitalized by molecular techniques and phylogenetic (cladistic) analysis. Therefore, to judge the significance of this book, the simple task is to assess whether it exemplifies or showcases these new trends in systematics. The simple answer is no. This book is mostly about where avian systematics has been and not about recent work or future directions. I would hope that this book is not presented to students considering research in avian systematics as a cutting edge exposé, as it poorly represents the field.

One of the high points of this book is Barrowclough's chapter. A variety of molecular techniques is available in systematics, each suited to different types of problems, or levels of taxonomic resolution. Barrowclough estimated the time it would take to solve various problems using each of several techniques, using the clever measure of "Ph.D. equivalents," that is, how many Ph.D. dissertation projects it would take to solve a given question using

a particular method. I recommend Barrowclough's chapter to anyone as an overview of the uses and limitations of molecular techniques.

Other interesting chapters include those by Panov, and LeCroy and Vuilleumier. Panov describes a situation regarding geographic variation and hybridization in wheatears. The study contained considerable data (unusual for the chapters in this book), and well reasoned analyses and interpretations. The paper by LeCroy and Vuilleumier describes some guidelines for describing new species, and rightly criticizes the recent description of a bird species based solely on its DNA and pictures of the bird prior to its release.

The description of the British Museum by Knox and Walters was very enlightening, albeit somewhat depressing. Given the modern emphasis on systematics, such as that embodied in the Systematics Agenda 2000 (e.g., Cracraft, 1991, Systematic Zoology 40:520–523), it is unconscionable to see the treatment of museums in Britain, and more recently in Canada (where curatorial staffs of the museums in Ottawa and Victoria were eliminated or cut drastically). Museums, and associated personnel trained in identification of specimens, taxonomy, and phylogenetic relationships, must form the framework of our attempt to preserve the earth's biota. Thus, it is ironic that the British Ornithologists' Club is celebrating its contributions to systematics and taxonomy when its government is strangling scientific research in its world-renowned museum.

Although there is much debate about species concepts today, most of the papers in this book either implicitly or explicitly follow the biological species concept. Two chapters specifically addressed species concepts. Haffer reviewed the history of species concepts in ornithology from the perspective of the biological species concept; hence, the review has a decided bias. Amadon and Short reviewed the species concept debate, but did not address most aspects of the current controversy. Thus, the current debate raging in many journals about species concepts is not revealed in this book. I recommend reading Donoghue (1985, Bryologist 88:172–181), De Queiroz and Donoghue (1988, Cladistics 4:317–338), Cracraft (1989, Pp. 28–59 *in* Speciation and its consequences [Otte, D., & J. A. Endler, eds., Sinauer Assoc., Inc., Sunderland, Massachusetts]), Frost and Hillis (1990, Herpetologica 46:87–104), and Davis and Nixon (Systematic Biology 41:421–435) to get a real flavor of the debate over species concepts.

Amadon and Short also suggested three new names for taxonomic categories: mesosubspecies, mesospecies and isospecies. They continue to support Amadon's older suggested category "quasi-monotypic genus," as well as others such as "megasubspecies" and "Biogeographical Unit (or Species)." Unfortunately, Amadon and Short's categories are arbitrary and subjective, and depend on individual intuition and experience. Such categories continue the "taxonomy-as-art" approach, whereas systematists are striving to make their field a more scientific endeavor. For example, "mesosubspecies" are those subspecies "not approaching species status." I do not see how one could objectively develop criteria for the recognition of this category; hence, I do not see its worth, nor the worth of these other arbitrary categories.

Bock's chapter presents his view of what systematists interested in phylogeny should be doing. Bock mentions that details of his method are contrary to the beliefs of many systematists, and notes that he has pointed this out many times in the past literature. Bock often misrepresents the field of phylogenetic systematics. For example, Bock says that PAUP and HENNIG86, two commonly used computer programs for phylogenetic inference, use "some type of correlation analysis . . ." Correlation analysis? Unless this was a *lapsus calami,* Bock's understanding of phylogenetic systematics is incomplete, as correlation analysis is a phenetic, not phylogenetic, procedure. If Bock confuses the phenetic and phylogenetic schools of systematics his criticism of either must be weighed accordingly. Bock's version of systematics requires skill to state hypotheses about phylogenetic relationships, and then

exercises called "functional-adaptive analyses" to determine if a particular character or character suite supports the stated hypothesis. I think that more than skill is required. For example, Bock asserts that a certain structure could not have evolved into another because it would not have been functional. Because we do not know what the transition states might have been, and the environments in which they existed and functioned, it requires imagination as well as skill to execute the Bockian school of systematics. Falsification of hypotheses via functional-adaptive analysis appears to be a subjective endeavor. Bock also purports to be able to assess the degree of confidence in his results, but his procedure will be mysterious to students of statistics used to more conventional views of "confidence," or to those that view topological congruence of trees as a measure of confidence in a phylogenetic hypothesis.

Other papers, such as those by Voous and Potapov, also criticize phylogenetic methods, but their criticisms are based on unfounded assertions or misrepresentations of cladistics. Voous suggests that "Pragmatic rather than scientific values should be attached to bird genera and their naming." Practitioners of phylogenetic systematics have spent a great deal of time discussing how a phylogeny could be translated into a classification, but I would wager that none of that discussion involved "pragmatic" components. Similarly, Potapov concludes that morphological characteristics are more important for classification than molecular (or other) ones, and that phylogenetic analysis plays a minor role. Potapov suggests that taxonomic rank is determined by overall degree of resemblance, judged subjectively. Modern classification studies rely on explicit phylogenetic analyses of characters, without weighting the results by subjective, personal assessments. I would point interested people to ornithological authors such as McKitrick, S. M. Lanyon, Prum, Mindell, Raikow, Cracraft, Livezey, and Seigel-Causey, to name a few, for examples of modern phylogenetic analyses and classifications of avian taxa.

A number of papers, such as those by Louette, Morel and Chappuis, and Clancey, discuss geographic variation, however, few exhibit any of the flavor of modern analyses. Most current studies of avian geographic variation employ explicit sampling methods and multivariate statistics, and sometimes biochemical assessments of patterns of geographic variation. I would direct interested persons to papers by Barrowclough, A. J. Baker, Christidis, N. K. Johnson, Rising, to name a few, for examples of modern studies of avian geographic variation.

After having read each paper in this book, I personally would not buy it (I would write for reprints of a few papers). I do not think that most libraries need it either. The book itself is not well constructed, and the glossy pages with sonograms are falling out of my copy. The British Ornithologists' Club has a long history of natural history and taxonomic research. It is unfortunate that this book badly misrepresents the modern state of systematics in general, and ornithology in particular.—Robert M. Zink.

The Birds of Konza. The Avian Ecology of the Tallgrass Prairie. By John L. Zimmerman. Univ. Press of Kansas, Lawrence, Kansas. 1993:186 pp., 8 black-and-white plates with captions, 22 numbered text figs., 13 tables, 3 appendices, 9 pp. literature cited, 6 pp. index. $19.95 (cloth).—Both the International Biological Program and the Long-Term Ecological Research program of the National Science Foundation have provided support for multi-year inventories of critical ecosystem types, including grasslands. Such funds have enabled John Zimmerman and his colleagues to collect, tabulate and analyze data from a variety of grassland habitats during the 1970s and 1980s. One such site is the Konza Prairie Natural Area which is located in east-central Kansas, owned by the Nature Conservancy and administered by Kansas State University. The Konza is a 3486 ha tract located in one

of the last major remnants of "virgin" tallgrass prairie. The management plan for the Konza includes various combinations of burned, non-burned, grazed and non-grazed treatments. These treatments, in turn, lead to a variety of localized habitats supporting, not surprisingly, a diverse avifauna.

After a series of extremely valuable and thought provoking technical-level publications dealing with his work in grasslands, Zimmerman has produced this book summarizing, primarily, data from 1981 through 1990. The book is written in a non-technical format designed to appeal to the general public. However, the nature of the material, the crisp organization, and the excellent presentation style are sufficient to keep professionals interested and, in fact, pique their curiosity. Certainly no one is better qualified to write such a book.

After a brief preface, which gives an overall introduction to the book as well as a cursory description of the field methods involved, Zimmerman gives a solid description of the natural history of the tallgrass prairie. The reader is introduced to concepts such as: these habitats are "more than just grass," they are not composed of a "unique flora," they contain few endemic species (none of which are grasses!) and the avifauna is derived from grassland habitats in other geographic areas. Based on bird distributions, Zimmerman divides the range of habitats into 4 major types: gallery forest, attenuated gallery forest, grasslands (either burned or unburned) and rock outcrop shrubs. The latter are mostly ignored in subsequent tables and figures. Birds species richness, abundance and relative frequency are tabulated by species and habitat type.

Chapter 2 gives an overview of grassland ecosystem as it relates to bird numbers. Long-term trends on the Konza are compared with data from the Breeding Bird Survey. A subsection of this chapter summarizes Zimmerman's cutting-edge work on Dickcissels (*Spiza americana*), which leaves us with a sense of foreboding that the future of this formerly abundant species is in jeopardy due to 'the detrimental impact of human activities." Chapters 3 and 4 give similar treatment to the avifauna of forest and rock outcrop, respectively, ecosystems found within the Konza.

Chapter 5 is entitled "Prairie-Chickens" and gives a brief life-history account of the Greater Prairie-Chicken (*Tympanauchus cupido*). Also included in this chapter, presumably as an unnumbered subsection, is a discussion of Migration. Given its location in the text, one might assume that this is also about Prairie-Chickens. However, this section deals with those species that "spend neither summer nor winter" on the Konza, nearly 50% of the observed species.

Chapter 6 presents the annotated checklist, obligatory in books of this genre, and covers species accounts from 1971 through 1992. This chapter will be of interest primarily to those individuals who will be "birding" the area. The Appendices present (1) a phenological checklist of the birds of Konza Prairie, (2) the vascular plants mentioned in the text and their scientific names and (3) a glossary (a handy reference which I will use repeatedly).

All in all, this book is informative, well written and well edited (of a random selection of 25 text references, all were found in the Literature Cited section). I was especially taken with Zimmerman's emotional/philosophical comments in the section "In Praise of Standing Dead." Having attended college during the sixties, this section reminded me of other impassioned pleas generated over the past 30 years. Certainly all people residing in the present biosphere would do well to heed his words, "We inflict suffering upon ourselves when we let our purposes interfere with the way the world works." Thank you Dr. Zimmerman.—Robert C. Whitmore.

Atlas of Breeding Birds of the Maritime Provinces. By J. Erskine Anthony. Nova Scotia Museum Program of the Department of Education in conjunction with Nimbus Publishing Limited, P.O. Box 9301, Station A, Halifax, Nova Scotia, Canada B3K 5N5. 1992:

x + 270 pp., 214 distribution maps, 188 black-and-white illustrations and breeding season bar charts, 10 geographic reference maps, 9 maps summarizing results, 3 overlay sheets, softbound. U.S. $29.95.—This is a handsome and thorough addition to the growing list of breeding bird atlas publications in North America. This Atlas incorporates most of the characteristics that have become standard and brings to the mixture several innovative and useful features. Collaboration by the three provinces and rapid progress from field work to publication make this a useful and timely work.

Climatological, geographic, and cultural features of the Maritime Provinces are briefly summarized in three introductory chapters as they relate to bird distributions. Maps and narrative descriptions of geographic patterns help explain disjunct distributions of, for example, northern-associated species such as Fox Sparrow along the Atlantic coast. Patterns described in these chapters become recurrent themes throughout the book. The description of cultural patterns provides insight into historical land use impacts on bird distributions. Tabular and mapped summaries briefly highlight what the project achieved. This atlas reports on the efforts of 1120 people spending over 43 thousand reported field hours in the 1682 sampling units, 10 × 10 km in size. Ninety-six percent of the 450 priority and special squares achieved adequate coverage, defined as 75% of expected species. Of the total 214 breeding species reported and mapped, 195 were confirmed and 10 "headline" birds were reported nesting for the first time. Seven historical nesting species were not recorded during the five-year effort.

A useful chapter, immediately preceding the species accounts, prepares the reader to use the accounts and warns of their general weaknesses. In conjunction with an earlier page entitled "How to read the atlas maps," the assorted elements found in each species account are explained. The introduction sometimes leaves the expectant reader hanging. For example, of the aforementioned "headline" species it is stated that "successful nests were found only for two." Which two? The answer can be found by searching tabular summaries in Appendix E or the species accounts. Although the introductory summary appears somewhat cursory and disjunct, the reader will discover chapters following the species accounts that complete the synopsis. Minor criticisms aside, the stage is set for an enlightened reading of individual species accounts and interpretation of results.

The 188 accounts of regularly occurring species are handsomely designed to present a variety of features laid out one page per species. Bi-color maps present atlas results at two mapping scales for each species: the sampling scale and a coarser scale (20 × 20 km resolution) as a smaller insert. Breeding evidence is presented by colored dots of three sizes, identified by a key on each page at the scale of the primary map. The maps are very legible and well drawn, with handsome background detail. Each account of regularly occurring species, labeled by English, French, and scientific names, is accompanied by a generally handsome pen-and-ink illustration by Azor Vienneau, a seasonal bar chart which illustrates normal dates of eggs and young, and estimates of breeding population size in the Maritimes and its provinces. Citations are not incorporated into the text, but reference numbers are listed at the end of most species accounts. The absence of citations for some species is disheartening. The references, although relatively few, generally are selected from studies within the region.

Each species account opens with a description of the worldwide range and a general statement of the range in the Maritime Provinces. Recent range changes and responses to European settlement place the results in temporal context. Habitats, nest-site characteristics, and food preferences were summarized where these relate to distribution patterns. Atlas results, in terms of number of squares, percent confirmations, and other notable results, are briefly mentioned in the text rather than in tabular summaries, sometimes resulting in cumbersome style and unclear statements. Distribution patterns are interpreted with generally

good insight. However, identifying the New Brunswick highlands as the "southern edge of the continental range" for the Blackpoll overlooks the disjunct population well documented by the New York breeding bird atlas (1988) in the Adirondack and Catskill mountains, more than 300 km to the south. Most species accounts end with notes on conservation issues and population trends. A wide range of comments conjecture on future status. In an extreme example, the Golden-crowned Kinglet account comments that "their long-range future here is uncertain." That, for a species found in more than 80% of squares, with an estimated population of 355,000 pairs, and an increasing BBS trend! A passing mention of nuclear wastelands and repetitious references to global warming sometimes diminish the environmental comments to rhetoric.

Brief accounts and a single map each for 26 species identified as peripheral and casual follow the main body of the work, two per page. Inclusion of Bohemian Waxwing in this section broadens the description of this section to include hypothetical species (by the author's own admission) and detracts from the list. Lists of past breeders, species with nonbreeding summer records, and recently introduced species conclude the species accounts. Thoughtful groupings of species by habitat and range limits are presented in chapter VII.

Four appendices provide technical references which make this among the best documented of published atlases. Features included here rival the documentation included in the Atlas Handbook, and make this a valuable reference for anyone interested in initiating an atlas effort. Descriptions of data processing and review demonstrate that this was a well designed project. Chapter VIII summarizes and explains the innovative population estimates computed for each species. The process of computing these estimates, described in Appendix D, is essential, but probably will leave most readers confused. The analytical technique appears to be valid, although caution should be used in interpreting the resulting estimates because of species detectability problems, subjective "trimming" of records and sampling intensity, all of which are acknowledged as issues. A final appendix includes five statistical tables, summarizing the raw data of the atlas.

This atlas was handsomely designed and packaged with the reader in mind. The publication will serve well the many birders that visit the Maritimes and is a grand tribute to the residents who labored to produce it. Covering an area toward the northeastern corner of the continent, the *Atlas of Breeding Birds of the Maritime Provinces* is an essential reference for anyone interested in bird distributions in North America.—Daniel W. Brauning.

The Human Nature of Birds. By Theodore Xenophon Barber. St. Martin's Press, New York. 1993:226 pp., 12 color photographs with captions (bound in center as 8 plates). $19.95 (U.S.), $26.99 (Canada).—It is said that anyone with a magnifying glass on a string around his or her neck must be a botanist, and I propose that anyone similarly adorned with the albatross of "instinctual" must be a psychologist. It is a perfectly valid dictionary entry, but in a world in which everyone else uses "instinctive" the reader knows from the very first paragraph of this book's Introduction that the author is a psychologist—although he describes himself in the opening sentence as "a behavioral scientist, with a professional reputation as a hard-headed skeptical researcher." The stereotypical psychologist's knowledge of avian behavior is restricted to the output record from a Skinner box within which a White Carneaux pigeon is pecking at an illuminated key, so *The Human Nature of Birds* portends an unusual viewpoint on the stated content of human-like cognitive capacities of our feathered friends.

The topics range widely: talking birds, food caching, tool using, territoriality, foraging, communication, song, migration and navigation, and so on. There is an appendix on the

"continuing cognitive ethology revolution" and another on "how you can personally experience a bird as an intelligent individual." A third appendix provides Latin names of species mentioned in the text, followed by "notes" (mainly references) serially numbered within chapters, and an index. It is a nice package but the white typeface within black banners at the top of each page and heading each chapter is often unreadable in my copy.

In any popularization such as this the paramount question is one of accuracy: are the facts and interpretations right, is the documentation sound? Given the enormous breadth of material, the author has done a reasonable job, but not a meticulous one. At the least one would hope for standard names of birds, spelled correctly—not such things as the "North American Nuthatch *Sitta pussila*" (p. 174) which is presumably the Brown-headed Nuthatch *Sitta pusilla* (one *s,* two *l*'s). I am not picking nits; with some 9000 species of birds in the world, it is an absolute requirement that we know which one is being discussed. The "great shearwater" of page 58 may be recognizable as the Greater Shearwater (*Puffinus gravis*) to those of us familiar with the European literature, but the former is not listed in Appendix C on "Scientific Names of Species" and the latter is given there under its nineteenth century generic name. Chapter five is about a hand-reared jay called a "scrub jay" (p. 40), but the popular book on which the chapter is based is entitled *Lorenzo the Magnificent: The Story of an Orphaned Blue Jay* (p. 191), so which is the right species?

The literature citations are impressive, but careful reading suggests that many are cribbed from secondary sources such as *The Life of Birds* by Welty and Baptista (e.g., scrutinize the notes on pp. 183–185). Was the author really able to read Homberg's paper about "Fiskande kråkor" (fishing Hooded Crows) as cited on p. 11 and listed on p. 182? When I list a paper in Swedish or Norwegian, I have (admittedly painfully) plowed my way through it; otherwise I tell the reader through whose eyes I think I know the content. The book clearly targets recent findings, continually touted as revolutionary, whereas some familiarity with original literature would have provided a more accurate setting. For example, the compressibility of territories is supposedly a new finding (p. 15), but in fact was announced to the world before I was born—by Julian Huxley in an immediately classic paper in *British Birds* in 1934 (not cited in this book, of course).

Which brings me to the "strawmanism" that permeates the volume. The book's thesis is provided up front, as they say, on the first page of the Introduction: "Since I had previously accepted the official scientific view that birds are instinctual automata, I was horrified to realize that I and virtually all other scientists have been blocked by the official taboo against anthropomorphism from perceiving the nature of reality, beginning with the intelligent nature of our close neighbors, the birds." That quote typifies the high-level confusion that dominates the structure of this book, so I will attempt partial disentanglement of this web with four specific points.

First, this reputedly "official scientific view" that birds are nothing more than little windup toys is a fignewton of the author's imagination. Over and over again in the book we are told of this view. It was never an official or even an unofficial view—in fact, never even a view—in the two sciences I dabble in, namely ethology and ornithology. So I am led to conclude that the author's brand of psychology must have official views and that those views are pretty naive when it comes to birds.

Second, any supposed taboo against anthropomorphism never inhibited the research of anyone I know. In fact, anthropomorphism is not even the issue in cognitive ethology. It is simply not scientific to attribute human characteristics to inanimate objects, animals, or natural phenomena and let it go at that. So in that sense, the taboo still exists.

Third, the real issue at stake has been how to identify and analyze complex behavior. Our advances have not all been sudden and recent, but rather episodic over a long period, and dependent upon the ingenuity of individual researchers, not the shedding of reputed

taboos. Ethology first had to prove that observed avian behavior must involve impressive complexities, and then to devise methods for analyzing those complexities. For example, Irene Pepperberg's comprehensive studies of Alex, a talking African Grey Parrot (*Psittacus erithacus*), have elucidated avian concept formation in a manner that no previous investigator could think of a way to approach. As clever as Alex is, remember that Pepperberg is really the clever one. In recounting Alex's story (pp. 4–8), the author misses this point entirely.

Last, this book seriously confounds a host of distinct concepts such as emotional organization, individual personalities, intelligence and cognitive abilities, human-like traits, sophisticated communication, and complex behavior. These are overlapping sets and just because given behavior has one of these attributes does not imply the others. Take for example an entire chapter devoted to avian navigation (pp. 58–73). The book promises (p. 3) to show that "birds are superior to humans in other kinds of intelligence (such as navigational intelligence)." I grant readily that many avian species are far superior to me, and presumably my conspecifics, in navigational abilities, but to confound this marvelous accomplishment with the notion of "intelligence" simply is not intelligent.

Even a disappointed reviewer has a responsibility to identify the good, so take this "did you know?" quiz. (1) When asked what object is red wood, Alex the parrot can pick it out from among various colors of wooden objects and various red objects made from cork, cloth, paper and so on. (2) Certain ground-nesting birds lead a potential predator away from the nest site by a "broken wing" distraction display. (3) Herons have been seen dropping bread onto water and then catching the fish that rise to nibble the bait. (4) Bird calls may "mean" different things to companions depending upon the context. (5) Bowerbirds decorate their structures with flowers and other colorful objects. (6) Homing pigeons and some diurnal migrants use a sun-compass in conjunction with an internal clock to help find their way. (7) Starlings can learn to imitate human speech and use certain phrases in appropriate contexts. (8) Some birds are known to engage in play behavior. That sample suffices. If you already knew those things, you probably would not learn much by reading this book. If such facts are new, then this book is as convenient a way to acquire them as any. Just read the specific accounts and ignore the relentless hyperbole about how everyone believed otherwise—and don't take species' identifications seriously.

The author's ultimate namesake, Xenophon (430?–355? B.C.), is remembered mainly for leading the retreat of the Ten Thousand from Persia in 401 B.C. Xenophon found only simple pleasure and delight in Athenian life, overlooking the deeper implications articulated by his older and somewhat brooding contemporary Thucydides. Our only knowledge of Socrates comes from Xenophon and his co-disciple Plato, the former respecting his master for the practical wisdom imparted, such as how to run a complex household efficiently, apparently missing entirely the philosophical content expounded by Plato. Oh, well, what's in a name?—Jack P. Hailman.

The Marin County Breeding Bird Atlas: A Distributional and Natural History of Coastal California Birds. By W. David Shuford. Bushtit Books, Bolinas, California. 1993: xv + 479 pp., many black-and-white sketches, maps. $24.95 + $3.50 S/H (obtainable from publisher, P.O. Box 233, Bolinas, California 94924).

Atlas of the Breeding Birds of Monterey County, California. Edited by Don Roberson and Chris Tenney. Monterey Peninsula Audubon Society, Carmel, California. 1993: viii + 438 pp., many black-and-white sketches, maps. $45 (hard cover), $19.95 (soft cover) (obtainable from the publisher, P.O. Box 985, Pacific Grove, California 93950).—As the

shelf of breeding bird atlases increases with additional publications we now have the first results from a western area. Unlike the other projects which have covered a state or province each of these two new atlases covers only a single California county. Monterey County, indeed, has a greater area than two of the eastern states whose atlases are in progress.

Both projects followed the now familiar atlas methodology except that Monterey County established their grid using the Universal Transverse Mercator grid rather than the usual U.S.G.S. 7.5 minute topographic map grid. Marin County divided the topographic sheet into 16 blocks rather than the six used by most eastern atlases. Marin managed to cover all the blocks in the county, but Monterey, having a much larger area and limited manpower, had to establish a priority system and did not cover all blocks.

The species accounts in both books are extensive, and are not forced into a fixed allotment of space for each. Besides summarizing the distribution varying amounts of natural history information are given, and both books discuss conservation matters. Each account in the Monterey book is accompanied by a black-and-white sketch of the species, done by 14 different artists.

It is in the "front matter" that both of these books differ from other atlases, and here they make their greatest contribution. Both include the seemingly obligatory history of atlasing, a summary of the physical environment, and the nitty-gritty of the local atlas organization. The habitats of the county are described in more detail than has been done in the state atlases so far published. In contrast to eastern areas, both of these counties have complicated mosaics of habitats. The habitats in Monterey County are classified in 24 types and for each a map of the atlas blocks containing some of the type is given. The descriptions of the 14 Marin habitat accounts are accompanied by delightful sketches of landscape by Ane Rovetta. These add greatly to the reader's appreciation of the coastal environment.

The Marin atlas contains a long detailed discussion of the results which includes a thorough analysis of the breeding birds of each of the habitat types. This synthesis of atlas results, which is sadly lacking in most published atlases, should be required reading for all students of avian distribution. The Monterey atlas has a shorter analysis. Together these discussions give the reader a vivid picture of the avifauna of coastal California.

Atlasers from the East who have suffered through long delays in publication of their work will be chagrined to notice that the field work for the Monterey atlas was completed in the summer of 1992 and the publication reaches us in the fall of 1993. This remarkable record was accomplished by such modern tools as the word processor and "Desktop Publishing" as well as the avoidance of state bureaucracies and commercial publishing firms.

I recommend both atlases to those interested in bird distribution, and especially to other atlasers whose work has not yet been published.—George A. Hall.

SHORT REVIEWS

Birds of Indianapolis. By Charles E. Keller and Timothy C. Keller. Indiana Univ. Press, Bloomington, Indiana. 1993:145 pp. 96 colored photos, 2 maps. $25 (cloth), $12.95 (paper).—A father-and-son team, the Kellers have produced an attractive addition to the local faunistic library. Short accounts are given for 125 of the most common birds to be seen in the eight-county area centered on Indianapolis, Indiana. There are excellent colored photographs of 96 species, taken by the junior author. The front matter contains suggestions for beginning birders and descriptions of a few birding spots. An appendix lists all the species known for the region. This publication should be useful for visiting birders or local neophytes.—G.A.H.

Status and Conservation of the Marbled Murrelet in North America. Edited by Harry R. Carter and Michael L. Morrison. Proceedings of the Western Foundation of Vertebrate Zoology, Volume 5, No. 1, Camarillo, California. 1992:133 pp. $20.—The discovery that the fate of the Marbled Murrelet (*Brachyrhamphus marmoratus*) like that of the Spotted Owl (*Strix occidentalis*) is tied with the future of the old growth forests of the Pacific Northwest has stimulated work on this seabird. The present volume consists mainly of the papers given at a 1987 meeting of the Pacific Seabird Group, but many of the papers were not submitted for publication until much later, the dating of the material is misleading. There are seven papers detailing the status of the murrelet in Alaska, British Columbia, Washington, Oregon, and California. An eighth paper discusses the capture and radio-tagging of murrelets. Perhaps the most useful contribution of the paper is 12-page bibliography of the murrelet, hopefully complete through January 1992.—G.A.H.

Perdix VI. First International Symposium on Partridges, Quails and Francolins. By M. Birkan, G. R. Potts, N. J. Aebischer and S. D. Dowell (eds). Gibier Faune Sauvage, 9: 283–918 (1992) (available from the Game Conservancy Trust, Fordingbridge, Hampshire, SP6 1EF, U.K. No price given).—The first 5 Perdix workshops were held in North America and were concerned exclusively with *Perdix perdix,* but the 1991 symposium broadened the coverage to include other Galliform species. Representatives from 26 countries met in Hampshire and we have before us this collection of 56 papers given there.—G.A.H.

Identification Guide to European Non-passerines. By Kevin Baker. British Trust for Ornithology Field Guide 24. Available from The National Centre for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, U.K. 1993:x + 332 pp., many black & white drawings. £15.—European bird ringers have had a useful guide to sexing and aging passerine species (see review, Wilson Bull., 105:544 [1993]), and now the B.T.O. has published an equally valuable treatment of the non-passerines. Since about 60 of the 119 species covered also occur in North America banders on this side of the Atlantic may find this publication of use.—G.A.H.

Birds of Prey in Virginia. An addendum to specimen records. By David W. Johnston and Roger B. Clapp. Virginia Avifauna No. 5, Virginia Society for Ornithology, Gloucester, VA. 1993:ii + 23 pp. $3.—Additions to Virginia Avifauna No. 4 (see review, Wilson Bull., 103:535 (1991).—G.A.H.

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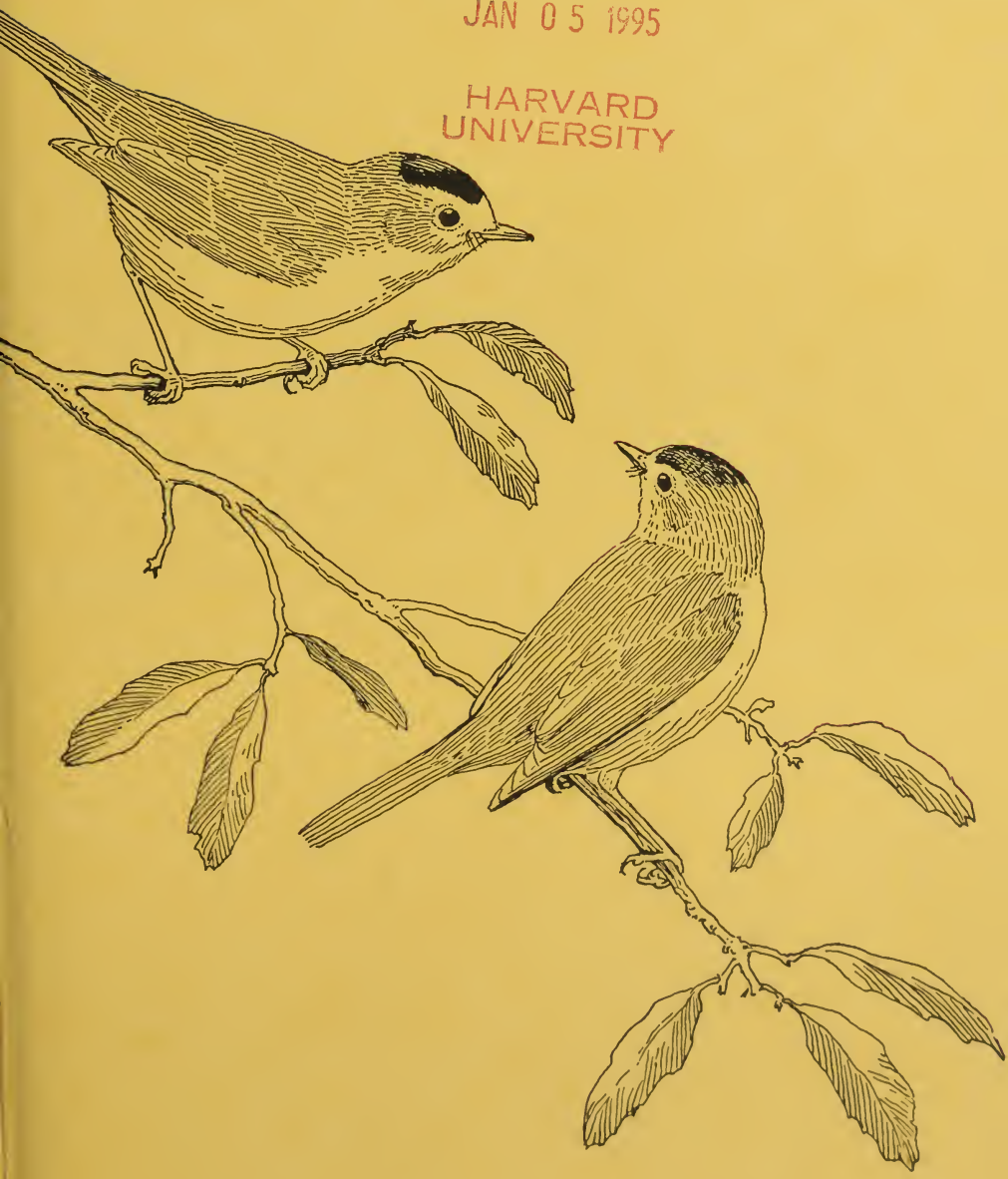

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Scytalopus schulenbergi sp. nov., a new tapaculo from the humid-temperate forests of Bolivia and southern Peru. Painting by Jon Fjeldså.

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A NEW *SCYTALOPUS* TAPACULO (RHINOCRYPTIDAE) FROM BOLIVIA, WITH NOTES ON OTHER BOLIVIAN MEMBERS OF THE GENUS AND THE *MAGELLANICUS* COMPLEX

BRET M. WHITNEY

ABSTRACT.—In Bolivia in 1992 I tape-recorded and observed several individuals of an undescribed tapaculo of the systematically complex genus *Scytalopus* in humid-temperate forest near the city of La Paz. During March 1993, Bolivian colleagues and I collected a series of the undescribed taxon from two geographically distinct regions of Depto. La Paz, and confirmed its presence as far south as Prov. Chapare, Depto. Cochabamba. The new species, the Diademed Tapaculo (*Scytalopus schulenbergi*), is described and its distribution and vocalizations are compared with some other members of the genus, mostly in Bolivia. I reexamine systematics of the *magellanicus* group and, based primarily upon striking and consistent vocal differences across the North Peruvian Low in northwestern Peru, I recommend its division into two superspecies with the names *magellanicus* (southern populations) and *griseicollis* (northern populations). *Received 22 July 1993, accepted 20 Feb. 1994.*

The genus *Scytalopus* spans the entire range of the Andes (as well as the mountains of southern Central America and the mountains and isolated serras of eastern Brazil southward to Misiones, Argentina), and appears to have undergone a particularly complex speciation (Zimmer 1939; Fjeldså and Krabbe 1990; Arctander and Fjeldså, in press; T. Schulenberg and N. Krabbe, pers. comm.). That *Scytalopus* has not colonized pantepui probably reflects poor dispersal capability, a factor that has contributed to a rapid and diverse speciation in the geographically complex Andes. The informative accounts of *Scytalopus* taxa in Fjeldså and Krabbe (1990) represent the first comprehensive treatment of the genus in the Andes, and provide the first organized insight into the several species groups and multiple lower taxa involved (see Vielliard 1990 for a recent

Field Guides Incorporated, P.O. Box 160723, Austin, Texas 78716-0723.

treatment of Brazilian taxa). A great deal of confusion persists, however, and the relationships of many taxa remain obscure. The complexity of recognition of the various forms within *Scytalopus* is perceptually confounded by a general lack of understanding of the manner in which taxa segregate behaviorally and spatially. These complexities derive from several sources. First, *Scytalopus* inhabits an incredibly wide latitudinal and elevational distribution, with one or more members on virtually every slope of every cordillera, which inherently introduces limitations to the resolution of data because adequate collections from many Andean localities, even those relatively accessible ones, do not and may never exist. Secondly, *Scytalopus* displays only minor differentiation mensurally (Table 1) or in plumage, with many (all?) species showing age-related plumage variation (species may take several years to attain definitive plumage; Fjeldså and Krabbe 1990:422) that is usually greater than interspecific variation; its taxonomy is based upon types sometimes lacking reliable locality and/or elevational data, and always lacking vocal data, such that some existing names may be of dubious application to other specimens, especially those taken any distance from the type locality; additionally, *Scytalopus* comprises more species-level taxa than currently recognized, probably considerably more (Fjeldså and Krabbe 1990:422; Arctander and Fjeldså, in press; T. Schulenberg, N. Krabbe, and D. Stotz, pers. comm., pers. obs.); more than one species occurs at many localities, sometimes syntopically; and *Scytalopus* tapaculos are notoriously difficult to observe in the field owing to the dense understory vegetation frequented by most species, and the skulking nature of the birds; finally, because many of the species sing at long and unpredictable intervals, it is difficult to adequately tape-record full, unsolicited songs for comparative purposes.

Given these realities, the complexities of species limits in *Scytalopus* may be resolved in large measure when it is recognized that (1) at no known locality does more than one species of *Scytalopus* inhabit habitats above the natural local treeline (well away from the ecotone with the forest); (2) at the vast majority of localities, no more than two species of *Scytalopus* occur in the same habitat at the same elevation (this is especially true when the very large, possibly generically distinct *S. macropus* is considered separately); (3) bands of species overlap are narrow with respect to the width of the local elevational distribution of the species involved; (4) symmetrical white markings on the head are probably important plumage characters (T. Schulenberg and N. Krabbe, pers. comm.); and that (5) songs and scolds are highly stereotypical within local populations, and seem to be reliable indicators of taxonomic limits in this suboscine genus (Fjeldså and Krabbe 1990; Vielliard 1990; Arctander and Fjeldså, in press), although slight vocal differences (but often no plumage

TABLE 1

MEASUREMENTS OF SELECTED *SCYTALOPUS TAPACULOS*

Taxon	Culmen		Tarsus		Wing chord		Tail	
	N	$\bar{x}$ (range)	N	$\bar{x}$ (range)	N	$\bar{x}$ (range)	N	$\bar{x}$ (range)
S. schulenbergi	26	10.8 (10.2–12.1)	26	21.7 (20.4–22.7)	26	51.0 (47.1–55.0)	25	37.5 (33.8–43.2)
S. argentifrons	2	11.5 (11.4–11.6)	2	20.6 (20.6)	2	50.6 (49.3–52.0)	2	38.5 (37.9–39.1)
Unnamed (Cuzco, Peru)	2	10.7 (10.4–11.0)	2	22.2 (21.7–22.8)	2	50.0 (50.0–50.1)	2	33.5 (32.4–34.7)
Unnamed (Pasco, Peru)	12	11.3 (10.7–11.7)	12	20.2 (18.9–21.2)	12	52.2 (50.4–54.2)	12	36.5 (33.6–38.5)
S. [m.] acutirostris simonsi	11	11.3 (10.3–12.7)	12	20.2 (18.7–21.9)	12	50.0 (46.4–53.1)	12	36.3 (33.7–41.0)
S. [u.] parvirostris	12	11.1 (10.1–11.8)	12	22.2 (21.0–23.0)	12	51.6 (50.1–54.3)	12	38.7 (34.8–43.8)

divergence) within taxa may be observed across natural habitat breaks (pers. obs.).

Because plumage appears to be more conservative (and certainly more confusing) than voice, and because vocal differences appear to be correlated closely with genetic differences (Arctander and Fjeldså, in press), I suspect that species limits within *Scytalopus* will be settled as satisfactorily by the correlation of habitat, elevation, and the presence of certain recurrent geographic barriers with marked vocal shifts, as by any other approach. Molecular analyses will eventually allow a test of the vocal and morphological data to the extent that molecular material is accompanied by specimens that also have been tape-recorded.

In February 1992, while conducting an avifaunal survey in humid-temperate forest on the east slope of the Andes just over the pass from the capital city of La Paz, Bolivia, I heard, tape-recorded, and saw an apparently undescribed *Scytalopus* tapaculo. In March 1993, together with Omar Rocha O. of the Museo Nacional de Historia Natural in La Paz, I obtained a series of this form, and made further tape recordings documenting various of its vocalizations. Consideration of this tapaculo's distribution, vocalizations and, to a lesser extent, plumages, informed through examination of currently recognized species limits in the genus *Scytalopus* both in Bolivia and elsewhere in the Andes, convinces me that it is a new taxon best described as a new species, which I propose to name:

Scytalopus schulenbergi sp. nov.

DIADEMED TAPACULO

HOLOTYPE.—Colección Boliviana de Fauna (hereafter CBF) No. 2636; subadult male from about 4 km west of Chuspipata along the main road between La Paz and Coroico ("Cotapata" of Remsen 1985), 16°19′S, 67°51′W, 3215 m, Province of Nor Yungas, Department of La Paz, Bolivia; 28 March 1993; collected by Bret M. Whitney. Voice specimen archived at Library of Natural Sounds (hereafter LNS), Cornell Lab of Ornithology, Ithaca, New York: LNS No. 63427. Blood sample housed at Zoological Museum, Univ. of Copenhagen, Denmark (hereafter ZMUC).

DIAGNOSIS.—*Plumage:* A typical member of the genus *Scytalopus,* showing little sexual dimorphism and significant age-related plumage variation. Adults distinguished from most congeners, including the sympatric *S.* [*magellanicus*] *acutirostris* (see below for nomenclature) and *S.* '*unicolor*' *parvirostris,* by silvery-white, transverse crescent on forecrown (hereafter called "diadem"; Frontispiece, Fig. 1A; this and other photos to be archived at VIREO, Academy of Natural Sciences of Philadelphia). Adults are most similar to *S. argentifrons* of Costa Rica and western Panama, differing in more silvery-whitish throat, and duller and less extensive brownish color and absence of distinct dark spots and/or bars on the flanks and undertail coverts, and differ from other taxa having a diadem (unnamed taxon in Depto. Pasco, Peru; unnamed taxon in Depto. Cuzco, Peru) by the aforementioned characters, by generally darker coloration (which may, however, be due to

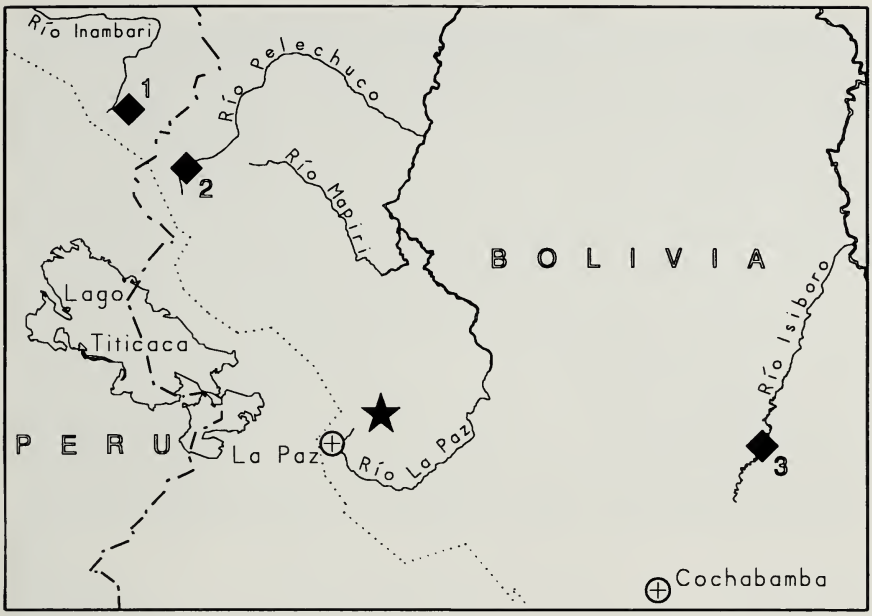

FIG. 1. Andes of extreme southern Peru south to central Bolivia, showing known localities for *Scytalopus schulenbergi*. 1. Valcón, Depto. Puno, Peru; 2. Pelechuco, Depto. Franz Tamayo, Bolivia; star, type locality (Cotapata), Depto. La Paz; 3. Prov. Chapare, Depto. Cochabamba. Broken line is Peru/Bolivia border. Dotted line is continental divide.

fading; see below), by longer tail (Table 1), and by absence of roughly concentric, alternating light and dark internal markings paralleling the margins of the rectrices. Adults further distinguished from *S.* [*m.*] *acutirostris* by the plain grayish tail (all ages of the latter show dark bars or other dark internal markings on the rectrices).

Juveniles are distinguished from *Scytalopus argentifrons* by generally paler coloration, and by much finer dark markings on individual feathers of head and body such as to appear barred throughout, lacking the scalloped pattern produced by wide, dark subapical lunules of *argentifrons*. They also appear to be distinguishable from [*m.*] *acutirostris* by dark subapical pattern of individual feathers of underparts: marked with a bar curving proximally to reach the feather margin in *schulenbergi*; marked with a wholly internal, teardrop-shaped band surrounding the feather shaft completely, enclosing a light-colored region along at least the distal portion of the shaft, in [*m.*] *acutirostris*. Differs from '*unicolor*' *parvirostris* by grayer crown to upper back of that species, and by the same individual feather characteristics of [*m.*] *acutirostris* described above, only heightened in degree in '*unicolor*' *parvirostris* by the greater width of these dark markings. Juveniles of *schulenbergi* having clearly barred central rectrices (as opposed to those marked with roughly concentric dark bands) may be distinguishable from both the latter two species by the presence of 7–8 thin dark bars as opposed to 3–5, relatively wider bars of the other two species. A larger sample will aid considerably in establishing the diagnosability of juvenal plumages.

DIAGNOSIS.—*Voice:* Full songs are distinguishable from those of all known congeners by the pattern of the first three or four seconds taken together with the overall duration of

the song (see sonagram figures). The scold and some other vocalizations are not 100% diagnosable.

DISTRIBUTION.—Known from as far north as Valcón, 14°16′S, 69°24′W, 3000 m, Department of Puno, Peru to as far south as approximately 16°30′S, 65°30′W, 3200 m, in the Province of Chapare, Department of Cochabamba, Bolivia, and two points in between: the type locality; and 5 km by trail east of Pelechuco, 14°48′S, 69°03′W, 3350 m, Province of Franz Tamayo, Department of La Paz (Fig. 2).

DESCRIPTION OF HOLOTYPE.—Forecrown marked by narrow (1.5 mm) frontlet of short, somewhat stiffened blackish feathers surrounding base of maxilla, bordered posteriorly by a partial, white diadem, the feathers of which are in obvious molt, widest on centerline of crown, and tapering laterally and posteriorly to a point above and behind eye, terminating approximately 2 mm behind posterior edge of orbit (Frontispiece, Fig. 1A). Diadem feathers with a reflective quality such that contrast and extent of diadem are seen to change relative to viewing angle. Diadem appears deepest (about 6 mm) and brightest from a superior, frontal angle, and narrowest and dullest when viewed from directly above or slightly behind. Crown posterior to diadem near Blackish Neutral Gray (capitalized color names from Smithe 1975). Lores same blackish color as narrow frontlet, this blackish extending posteriorly to narrowly surround eye. Nape and entire dorsal surface washed lightly with dull brown, most heavily along centerline of back and continuing to the rump. Scapular region more nearly approaches Blackish Neutral Gray color of crown. Chin and throat to a point approximately 7 mm posterior to base of mandible, silvery-gray with a reflective quality, grayer than diadem and, when viewed from the front, contrasting with blackish sides of head and, to a lesser extent, rest of underparts. Throat, when viewed from lateral or posterior perspective, appears close to Medium Neutral Gray, and contrasts less with dark feathering of the face and remainder of underparts. Underparts from base of throat to lower belly and including sides of breast and sides, near Dark Neutral Gray, displaying a silvery, graphite-like sheen on the feather margins, palest on the lower belly. Flanks and undertail coverts unmarked dull orange-rufous anteriorly, becoming weakly but increasingly barred posteriorly, the pattern of each feather consisting of two dark gray subapical bars, the most proximal of which sometimes surrounds the feather shaft blending into the dark gray base of the feather. Feathers of flanks, and especially those of lower back, much elongated (to 27 mm), loosely integrated, and somewhat downy in composition. Rump same dull orange-rufous as flanks and undertail coverts and similarly barred; uppertail coverts grayer with a weak orangish tinge, especially basally, and a hint of the barred pattern seen on the rump. Tail near Blackish Neutral Gray with a faint brownish cast. Rectrices lacking any pattern of barring or internal marking, but each having a minute brownish fringe anterior to tip. Wings, including all coverts, also Blackish Neutral Gray except two innermost tertials, which are mostly dull brownish with one subapical, dark gray bar on distal web. Other remiges with a narrow brownish fringe on proximal portion of distal web, imparting a weak brownish cast to folded wing. Soft parts in life: iris dark brown; tarsi and feet dark yellowish-brown; maxilla black; mandible dark brownish-black, slightly paler at base. Although it is not the best plumage example available (being a subadult in heavy molt), CBF No. 2636 was selected for the holotype because it was tape-recorded and a blood sample was obtained.

MEASUREMENTS OF HOLOTYPE.—Wing (chord) 48.9 mm; tail 38.3 mm; culmen from base (at skull) 10.3 mm; tarsus 20.4 mm; weight 15.2 g.

DESCRIPTION OF FEMALE.—The following is based upon paratype, CBF No. 2629. Similar to holotype. Differs from adult male by diadem both duller and reduced in the center, and by somewhat duller silvery throat. Upperparts entirely dingy brownish-gray, brownest in nuchal region. Uppertail coverts, flanks, and undertail coverts dull brownish

FIG. 2. A. Adult male *Scytalopus schulenbergi*, showing silvery-white diadem, pale throat, and blackish mask. B. Dense, somewhat stunted humid-temperate forest at 3300 m along the Rio Pelechuco in northern Bolivia, habitat of *S. schulenbergi*. *S.* [*magellanicus*] *acutirostris* replaces *schulenbergi* above treeline in rocky shrub/grassland, visible here on the upper slopes of the valley.

marked with two or three inconspicuous dark gray bars. Remiges with slight brownish tinge, especially toward margins. Soft parts as in males.

DESCRIPTION OF JUVENILE.—No indication of diadem or mask. Generally golden-brown, darker dorsally than ventrally, and reflective sheen on feathers obsolete. Every feather of head and body with a conspicuous dark subapical marking, over almost the entire upperparts, face, throat and upper breast in the form of a single, small Dark Neutral Gray spot at the most distal furcation of barbs on the feather shaft, but scapulars marked with a short streak along the shaft. Through remainder of underparts, subapical spot broadening and thickening slightly to become a bar. Elongated flank feathers, belly, and undertail covert feathers each marked with two or three bars that curve slightly proximally toward feather margin, producing a weakly lunulated pattern, most pronounced on belly. Tail dark golden-brown, each rectrix with seven or eight narrow, transverse bars or, apparently more rarely, two or three roughly concentric internal bands. Wing coverts with dark markings expanded greatly to cover proximal web of each feather to tip, leaving a relatively bright, golden-brown crescent at tip of distal web, coverts together forming fairly conspicuous, black-bordered wing-bars, most pronounced on greater primary coverts. Remiges near Dark Neutral Gray edged golden-brown, with margins soft and barbs weakly integrated; some individuals show light and dark spots on the distal webs of the outer primaries. Each tertial with a conspicuous subterminal bar curving proximally inside feather margin, and expanding to feather tip in a narrow point along shaft, producing, in effect, a series of black-bordered, pale crescents overlying folded wings. Soft parts as in adults, except legs decidedly yellowish.

SKIN SPECIMENS EXAMINED.—*S. schulenbergi*: Peru: Puno, Valcón, 6 ♂♂ and 3 ♀♀ (Louisiana State Univ. Museum of Natural Science [hereafter LSUMNS] No. 98394, 98395, 98396, 98399, 98400, 98401, 98402, 98406, 98407); Bolivia: La Paz, Prov. Franz Tamayo, 1 ♂ and 1 sex unknown (CBF No. 2640, 2641); La Paz, Prov. Nor Yungas, 8 ♂♂, 3 ♀♀, 3 sex unknown (CBF No. 2624–2630, 2632, 2633, 2636, 2637; LSUMNS No. 96092, 102258, 102261), and 1 sex unknown in alcohol (CBF No. 2631); Cochabamba, Prov. Chapare, 2 sex unknown juveniles (LSUMNS No. 37776, 37780). *S. argentifrons*: Costa Rica, Prov. San José, 1 ♂; Prov. Cartago, 2 ♂♂; Prov. Heredia, 1 ♀ (LSUMNS No. 62660, 135543, 135544, 138717). *Unnamed taxon*: Peru: Pasco, various localities near Depto. Huanuco border (Marín, Millpo, Abra Portachuelo), 16 ♂♂ and 2 ♀♀ (LSUMNS No. 128613–128629; Museo de Historia Natural Javier Prado, Lima, Peru No. 7333); Huanuco, within 2 km of Depto. Pasco border, 3 ♂♂ and 2 ♀♀ (LSUMNS No. 128608–128612). *Unnamed taxon*: Cuzco, 14 km NE Abra Málaga, 1 ♂ and 1 ♀ (LSUMNS No. 78579, 78580). *S.* [*magellanicus*] *acutirostris*: Peru: Puno, Valcón, 2 ♂♂ and 3 ♀♀ (LSUMNS No. 98397, 98398, 98403, 98404, 98405). Bolivia: La Paz, Prov. Franz Tamayo, 1 ♂ and 1 ♀ (CBF No. 2642, 2644); La Paz, Prov. Nor Yungas, 1 ♂, 1 ♀, and 1 sex unknown (CBF No. 2634; LSUMNS No. 90751, 96091); Cochabamba, Prov. Chapare, 2 ♂♂ and 1 sex unknown (LSUMNS No. 36130, 37775, 37779); Prov. Arani, 2 ♂♂ (LSUMNS No. 124233, 124234). *S.* [*m.*] *superciliaris zimmeri/acutirostris* intergrade(?): Bolivia: Cochabamba, Colomi, 1 ♀ (LSUMNS No. 37781). *S.* [*m.*] *magellanicus*: Argentina: Rio Negro, 2 ♂♂ and 1 ♀ (LSUMNS No. 25099, 25100, 70003). *S.* '*unicolor*' *parvirostris*: Bolivia: Prov. Franz Tamayo, 1 ♀ (CBF No. 2646; probably not true *parvirostris,* see below); La Paz, Prov. Nor Yungas, 5 ♂♂, 3 ♀♀, and 2 sex unknown (CBF No. 2635; LSUMNS No. 90750, 102254, 102255, 102256, 102257, 102259, 102260, 102262, 102263); Cochabamba, Prov. Chapare, 1 ♂ and 1 sex unknown (LSUMNS No. 36133, 37778). *S.* '*femoralis*' *bolivianus*: Peru, Puno, Abra de Maruncunca, 1 ♂ (LSUMNS No. 98393); Bolivia: La Paz, Serrania de Bellavista, 1 ♂ (LSUMNS No. 90749); La Paz, Prov. B. Saavedra, 2 ♂♂ and 1 ♀ (LSUMNS

uncataloged specimens from 1993); Sana Cruz, Samaipata, 1 sex unknown (LSUMNS No. 37773).

VOICE SPECIMENS EXAMINED.—All recordings made by the author unless otherwise indicated. *S. schulenbergi*: Bolivia: La Paz, 27 (representing more than 30 individuals, including CBF No. 2624, 2625, 2633 [juv scolds], 2636 [LNS No. 63427], 2640 [juv songs], and 2641); Cochabamba, 2 (representing probably 3 individuals). *S. argentifrons*: Costa Rica: Puntarenas, 3; Panama: Chiriqui, 2. *Unnamed taxon*: Peru: Pasco, 3 (including LSUMNS No. 128629; 3 G. Rosenberg). *S.* [*magellanicus*] *acutirostris*: Peru: Cuzco, 2 (representing 3 individuals); Bolivia: La Paz, 10 (representing 9 individuals, including CBF No. 2634 and 2644); Cochabamba, 9 (representing 6 individuals; 1 R. A. Rowlett); *S.* [*m.*] *superciliaris*: Argentina: Tucumán, 2 (representing 3 individuals; 1 D. Stejskal); *S.* [*m.*] *fuscus*: Chile: Santiago, 2 (1 G. Egli); *S.* [*m.*]. *magellanicus*: Argentina: Tierra del Fuego, 2 (1 J. Arvin); Chile: Malleco, 2. *S.* '*unicolor*' *parvirostris*: Bolivia: La Paz, 3 (including CBF No. 2635); Cochabamba, 3; Santa Cruz, 5. *S.* '*femoralis*' *bolivianus*: Bolivia: La Paz, 2 (representing 1 individual); Cochabamba, 3 (1 R. A. Rowlett). All recordings made by the author have been or will be archived at LNS. All recordings of collected birds will also be archived at the respective institutions where the skins are held.

BIOCHEMICAL SPECIMENS.—*S. schulenbergi*: Peru: Puno, two tissues (LSUMNS No. B-501 and B-522); Bolivia: Franz Tamayo, two blood samples (CBF No. 2640 and 2641); La Paz, two blood samples (CBF No. 2636 and 2637). Blood samples stored in APS buffer at ZMUC.

ETYMOLOGY.—I am pleased to name this new tapaculo after my friend and colleague Thomas S. Schulenberg, whose field work and informed insights have, for more than a decade, greatly aided many investigators in pursuit of knowledge of Andean birds. In 1980, he headed the LSUMNS expedition into the remote area of Valcón in Puno, Peru, that brought back a fine series of the new species. Finally, it was Tom who several years ago first encouraged me to delve into the depths of *Scytalopus*.

The proposed English name, Diademed Tapaculo, refers to the shining-white, crescent-shaped band marking the forecrown of adults of the new species, which occurs predominantly in Bolivia. Should the similarly "diademed" (but presently unnamed) tapaculo inhabiting the Abra Málaga region of central Peru (see below) eventually prove to be related to but specifically distinct from *schulenbergi,* I suggest the names Bolivian Diademed Tapaculo for *S. schulenbergi,* and Peruvian Diademed Tapaculo for the Abra Málaga bird.

REMARKS

Variation in the type series.—I restrict the type series to those (10) specimens collected at the type locality in 1993. This limitation ensures that the series contains truly comparable material, eliminating variation introduced by such factors as age of the prepared specimens, which may be significant (see below). Among males, the most consistent variation from the holotype is seen in the flanks and undertail coverts, which are washed more extensively and brightly with dull orangish-brown on some specimens, more weakly on others, but with barring, ranging from very weak to well-defined, present on all except one. This latter specimen (CBF No. 2632) is probably an adult in definitive plumage, and shows only a very weak tinge of brownish in the flanks and undertail coverts, and no trace of barring. The most conspicuous variation among males,

however, is seen in the extent and brightness of the diadem. In relation to the holotype, four have a more extensive diadem (two of these having diadems covering almost the entire front half of the crown), and two have reduced and significantly duller diadems, more similar to that of the holotype. Otherwise, males vary little from the holotype except that some are washed more extensively with dull brownish through the upperparts, concentrated on the lower back and rump. These specimens also show the most color and barring on the flanks and undertail coverts, and include the specimens with the smallest and dullest diadems. These birds, like the holotype, are probably subadults.

The series contains two specimens that are unequivocally in subadult and juvenal plumages, respectively; the latter is described above. The subadult (CBF No. 2627, sex unknown) was in molt of the head and body but not the wing or tail. The head, which was largely destroyed by shot, is generally brownish, with the center of the crown slightly grayer and a faint indication of a silvery diadem. The upperparts are as in the juvenal plumage, but the feathers of the neck, throat, and breast have been replaced with feathers of Medium Neutral Gray, the lower of which have narrow buff fringes. Additionally, some of the large, dull orangish-brown feathers of the lower sides (flanks?) are marked with two bars that curve proximally inside the feather margin to form a pattern distinct from that of juveniles or adults. The wing feathers appear to be newly replaced, but the tail is somewhat abraded and is likely the juvenal plumage. The wing-coverts are brownish-gray, except for a golden fringe and dark subapical spot on the distal web of each of the greater primary coverts, producing a faint wing-bar. The remiges lack the weakly integrated fringes and the light-spotted pattern on the edges of the distal webs of the juvenal remiges but are overall somewhat browner than those of older birds. This individual was not tape-recorded, but I heard it give a single loud "tek!" note that I have definitely associated with *S. schulenbergi.* As a final note, one specimen (CBF No. 2630) shows a single white feather on the side of the neck. Asymmetrical albinism of this nature is fairly frequent among *Scytalopus* (N. Krabbe and T. Schulenberg, pers. comm.).

Variation among the 18 additional specimens of *S. schulenbergi* examined is similar to that observed in the type series. In comparison with specimens from the type locality, those from Puno, Peru, and Prov. Franz Tamayo, Bolivia, may have slightly reduced diadems. The single juvenile from Franz Tamayo has a distinctly buffier throat than the one from the type locality. Among the predominantly gray-bodied *S. schulenbergi* examined, there is a consistent difference in general coloration between the birds collected in 1993 (nine; eight from the type locality, and one from

Franz Tamayo) and those collected in 1980 and 1981 (11; two from the type locality and nine from Puno, Peru). The more recent specimens are darker throughout, especially in the underparts, which are near Dark Neutral Gray, whereas the older specimens are all closer to Medium Neutral Gray through the underparts. Furthermore, the flanks and undertail coverts of the older specimens are lighter in color, more orangish and less brownish. These apparent differences are of the order of magnitude considered by Zimmer (1939) to warrant subspecific recognition. Because of the overlap of the localities involved, however, I have no doubt that these differences are due to the age of the specimens ("foxing").

Breeding and molt.—None of the specimens collected in March was in breeding condition (largest testis measured 5 × 2.5 mm). Gonads of most specimens were described as "little developed" (O. Rocha O. on specimen labels). We did encounter several juvenile *S. schulenbergi,* the plumage of which was advanced only a little beyond full juvenal, suggesting that they had fledged recently (although it is not known how long this plumage is retained or whether there is intraspecific variation in timing of the onset of post-juvenal molt). Judging from the few specimens available, the post-juvenal molt commences with the feathers of the head, throat, and breast, and it is probably this molt that produces the earliest indications of the silvery diadem (as discussed earlier with respect to subadult plumage). Aside from the juveniles, all March specimens showed conspicuous molt of some part of the plumage, and most birds in adult or near-adult plumages were in extensive molt of the entire plumage. Except for a few songs given early in the morning, *S. schulenbergi* was singing very little in late February and March (especially little on rainy days), less than I would expect if the birds were actively engaged in territorial activities. None of three La Paz *S. schulenbergi* collected 1 June, 31 July, and 4 August is in breeding condition; data on molt are lacking. The series of nine birds from Puno, Peru, taken in October may be considered to be in breeding condition, with testes ranging in size from 7 × 4 to 10 × 4 mm, and ovaries well developed. One female was observed "bringing food to nest." This nest and the two nestlings it held were collected (T. Schulenberg, pers. comm.; LSUMNS Egg and Nest Collection No. 907), and the nest was described as that of *Scytalopus magellanicus* by Rosenberg (1986). No data on vocalizations or molt were recorded on the Puno specimen labels. These considerations suggest that breeding takes place primarily between September and January, although data are lacking (aside from one specimen) for the period April to August.

Habitat and ecology.—*Scytalopus schulenbergi* lives only inside and at the edge of humid-temperate "cloud forest" and "elfin" forest and is so far known only from the east slope of the Andes. It does not occur in

habitats above the local treeline (whether natural or man-altered), although I expect that individuals wander a short distance out of the forest proper into the shrubby forest/grassland ecotone. All of the four known localities of occurrence are characterized by steep, forested slopes at or near treeline (Fig. 1B).

Remsen (1985) provided an excellent description of the habitat at the type locality of *S. schulenbergi* near Chuspipata, La Paz. His account covered two somewhat different sites about 5 km apart, one at 3050 m (Chuspipata) and the other at 3300 m (Cotapata). *S. schulenbergi* is common at both sites, but is especially common, and the only *Scytalopus* present, at Cotapata (the type locality). As noted by Remsen (1985), *Chusquea* sp. bamboo is abundant in the area, especially at Chuspipata, where the forest is more heavily disturbed by both natural landslides and selective logging (pers. obs.). *S. schulenbergi* does not appear to inhabit patches of *Chusquea* preferentially over areas of the understory dominated by other plants. It does seem to be partial to small ravines, perhaps especially those with a seepage of water, and bamboo is often dominant at such sites. The habitat description provided by Remsen (1985) applies closely to the other known localities of occurrence of *S. schulenbergi* in Bolivia, except that the site below Pelechuco in Prov. Franz Tamayo has suffered considerably more forest disturbance through cutting for firewood and fragmentation for garden space. *S. schulenbergi* appears to be much less common at this site.

The elevational range of *S. schulenbergi,* which is between about 2975 and 3400 m, overlaps that of two congeners, one at either extreme. *S.* [*m.*] *acutirostris* occurs primarily in the shrub/grassland above treeline (whether natural or not) but extends as low as the local limit of forest, penetrating the forest border wherever connected grassy or rocky openings permit. Thus it occurs alongside *schulenbergi* throughout the range of the latter (documented with specimens and tape at all known localities for *schulenbergi*), and the two can often be heard from the same position near the grassland/forest ecotone. It is the habitat more than the absolute elevation that determines the local elevational limits of these two taxa (e.g., north- and south-facing slopes of a wide canyon often have the natural grassland/forest ecotone at significantly different elevations; this ecotone around "treeline" in the Andes has been altered extensively by man). In the vicinity of Chuspipata, La Paz, *S.* '*unicolor*' *parvirostris* reaches its upper elevational limit at approximately 3100 m and is common as high as just over 3000 m. In the narrow band between about 2975 and 3100 m, it occupies the same habitat as *schulenbergi* and on occasion the two can be heard in exactly the same place. It appears that the slightly larger *parvirostris* (Table 1) is the dominant or more aggressive of the

two, because playback of *schulenbergi* songs or scolds within the overlap zone were (in late March, at least) more likely to elicit a response from *parvirostris* than *schulenbergi,* but playback of *parvirostris* vocalizations elicited response only from *parvirostris.* This may have as much to do with the species' respective (and largely unknown) breeding seasons as anything else. The only other insectivore that forages primarily on or very near the ground within the latitudinal and elevational distribution of *S. schulenbergi* is the Rufous Antpitta (*Grallaria rufula*) (Formicariidae), which has a considerably larger body mass. The Stripe-headed Finch (*Atlapetes torquatus*) barely overlaps *S. schulenbergi* at the lowest elevations (Remsen 1985; pers. obs.)

Foraging and other behaviors.—S. schulenbergi, like all members of the genus, was quite difficult to observe in an undisturbed foraging routine; for most individuals, I managed to make only general, brief (less than 5 sec) foraging observations. The following information comes from a single adult that at first had been scolding me but which I subsequently kept more-or-less in view for about 10 min as it unconcernedly foraged around me in a relatively open place in the undergrowth. This bird remained within about 50 cm of the ground the entire time, almost always within about 20 cm, and came down onto the ground several times. It moved slowly with very short hops, perching briefly on both horizontal and (less often) vertical perches, holding its tail at a relaxed angle (not cocked), and stopping briefly to scan the surrounding mossy ground, branches, and vegetation. It occasionally reached to and gleaned from these substrates (terminology follows Remsen and Robinson 1990) and also probed the moss coating thin vertical trunks and dead branches, usually spending less than 3 sec at such a site. While on the ground, the bird performed the above maneuvers and seemed to explore the upper few mm of the leaf litter visually and with light probes. It did not scratch or otherwise manipulate the leaf-litter or moss with its feet and did not reach to vegetation significantly overhead (such as the undersides of leaves). While I was standing on the trail after observing the above behaviors, the bird again appeared, hopping out into the middle of the 1.5 m-wide trail, where it froze with the tail cocked sharply over the back, then fluttered weakly up to the edge of a 2.5 m-high bank and resumed foraging somewhat more actively on mossy limbs about 30 cm above ground (from which position it could keep an eye on me below). No other birds were seen in the vicinity during these observations. The bird's white diadem was conspicuous as it moved through the dark understory, which may help members of a pair to keep in visual contact without vocalizing.

Three *S. schulenbergi* specimen labels indicate that the stomachs contained insects; no other stomach contents were recorded. The 14 stomachs

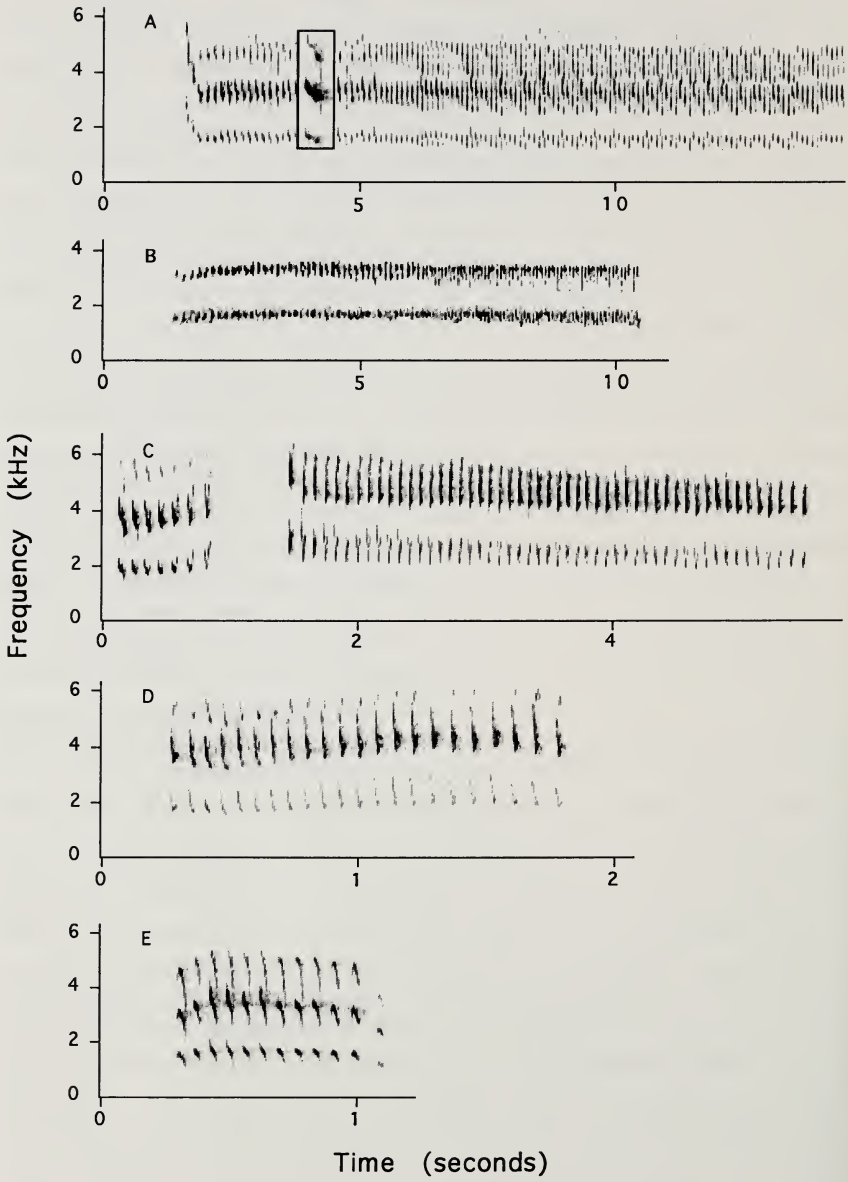

FIG. 3. Some vocalizations of *Scytalopus schulenbergi* from type locality for comparison with those of other taxa shown in subsequent figures. A. Adult male, song after playback, but one of natural variants; first 12.7 sec of 13.5 sec song (length variable); first one or two, burry syllables missed, end same as part shown. Noticeable 6-syllable pattern beginning at 6-sec point (repeated slants down to right) is not audible, and probably represents the bird's

collected in March 1993 have been preserved in alcohol at CBF, but have not yet been analyzed.

S. schulenbergi sings from a perch between about 20 cm and 3 m above ground on a horizontal limb, holding the head up and the tail pointing mostly toward the ground but not straight down. The throat is puffed out somewhat and the bill is opened only slightly. After playback of songs, males usually approached the tape recorder within 3 min, and in a couple of instances, climbed to as high as about 7 m above ground before singing in response. On several occasions, males appeared after tape playback, but did not vocalize. The single female collected in March responded to tape playback of its own scolds (Fig. 3D, E).

Were it not for its conspicuous voice and predictable response to tape playback, *S. schulenbergi* would be very difficult to detect and capture. In 17,587 daylight net-h (and an equal number of nighttime hours) at two sites in the humid-temperate forest near Chuspipata, La Paz (Remsen 1985), where *schulenbergi* is one of the most common birds in the forest undergrowth along roads and trails (pers. obs.), only two individuals were captured, and several hundred man-h (mostly without tape recorders) produced only one specimen shot. This is certainly understandable, considering the skulking nature of *Scytalopus* tapaculos in general, their reluctance to fly even short distances, and their generally slow progression through the undergrowth as they forage independently with near-perch maneuvers, allowing them to detect a mist-net the first time it is encountered (after the first encounter, entanglement in the net is probably very unlikely). Capture of the single specimen we netted required careful net-site selection and the practiced use of a tape recorder. Even then, the bird obviously avoided the net on the first pass and later became lightly entangled only in the lowest part of the net, the bottom several cm of which we had arranged on the ground, when it attempted to crawl under it. As the behavior of *schulenbergi* does not appear to differ significantly from

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breathing interval (recording made at ideal level, 5 m range, at 15 i.p.s.); 3380 m, 02 Mar 1993; CBF 2624. Inset in song of this and other figures represents an individual note/phrase (bisyllabic in some taxa) enlarged on time scale (same scale for all figures) to show more comparative detail. B. Age/sex unknown, complete natural song, with slow first half (and low beginning) and rapid second half; bird distant from microphone. 3100 m, 24 Feb 1992. C. Subadult, complete descending-series song, with sharp, rising-series introduction; after playback. 3190 m, 28 Mar 1993; CBF 2637. D. Adult female, excited scold soon after playback. E. Same adult female, scold typical of species, given by both sexes and all ages. 3395 m, 02 Mar 1993; CBF 2629. Sonagrams produced with "SoundEdit" of Farallon Computing, Inc., Emeryville, California, and "Canary" of the Bioacoustics Research Program at the Cornell Lab of Ornithology, Ithaca, New York.

that of forest-based congeners (pers. obs., although it may prove to be somewhat more arboreal, and it seems easier to see with tape playback than most), it is easy to imagine that avifaunal surveys (especially brief ones) that have not used tape recorders routinely could have missed some of these forest-based *Scytalopus* and possibly some of the taxa above treeline as well.

Vocalizations.—Almost all of the vocalizations of *S. schulenbergi* are distinctive and may be used to diagnose it from congeners more reliably than its various plumages. The primary song is a level series (sometimes dropping or rising slightly through the first few syllables) of very closely spaced syllables at about 3.3 kHz, lasting between about 7–15 sec, averaging about 9 sec. The song begins with 4–5 slightly burry or throaty syllables spaced far enough apart to be counted easily, after which it accelerates steadily for several seconds, either continuing at an even rate to the end of the song (Fig. 3A; first couple of notes missed) or sometimes abruptly accelerating once again in the final half (Fig. 3B). Songs delivered in response to tape playback are often considerably longer (up to 48 sec) and usually have scattered stutters in the series. This song apparently is given by individuals of any age, judging from a juvenile that was tape-recorded delivering it (albeit in response to playback) and collected (CBF No. 2640; sex unknown). I do not know whether females sing, but my observations suggest that they do not. A second song-type is a rapidly delivered, steadily descending series lasting 3–5 sec, often preceded by either a few loud, hard "tek!" syllables spaced 1–2 sec apart or, especially after tape playback, a rapid, sharp, rising series of syllables lasting about 0.5 sec (Fig. 3C). I suspect that this vocalization is given only by subadult birds, perhaps those less than one year old. Each instance in which I was able to see the bird that had definitely given this descending series, it proved to be either a juvenile or a bird in a plumage not far advanced from the juvenal (N = 6, 1 collected [CBF No. 2637]). To my knowledge, such noticeable age-related variation in the song has not been reported among suboscines (in fact, the contrary is the norm); I wish merely to report the possibility of its involvement in this case. In any event, I believe that this descending series is indeed a song in the sense that songs have been described in the genus, as it is delivered only once, at long intervals, from a perch above ground, and in the singing posture described above. All these songs differ appreciably from those of other *Scytalopus* taxa (compare Fig. 3A–C with Fig. 4A–C, Fig. 5A, and Fig. 6A), especially the sympatric *S.* [*m.*] *acutirostris* and *S.* '*unicolor*' *parvirostris.*

S. schulenbergi also frequently gives a scold or mobbing vocalization, heard most often when an individual is startled or disturbed by an observer, or in response to tape playback. A bout of scolding/mobbing may

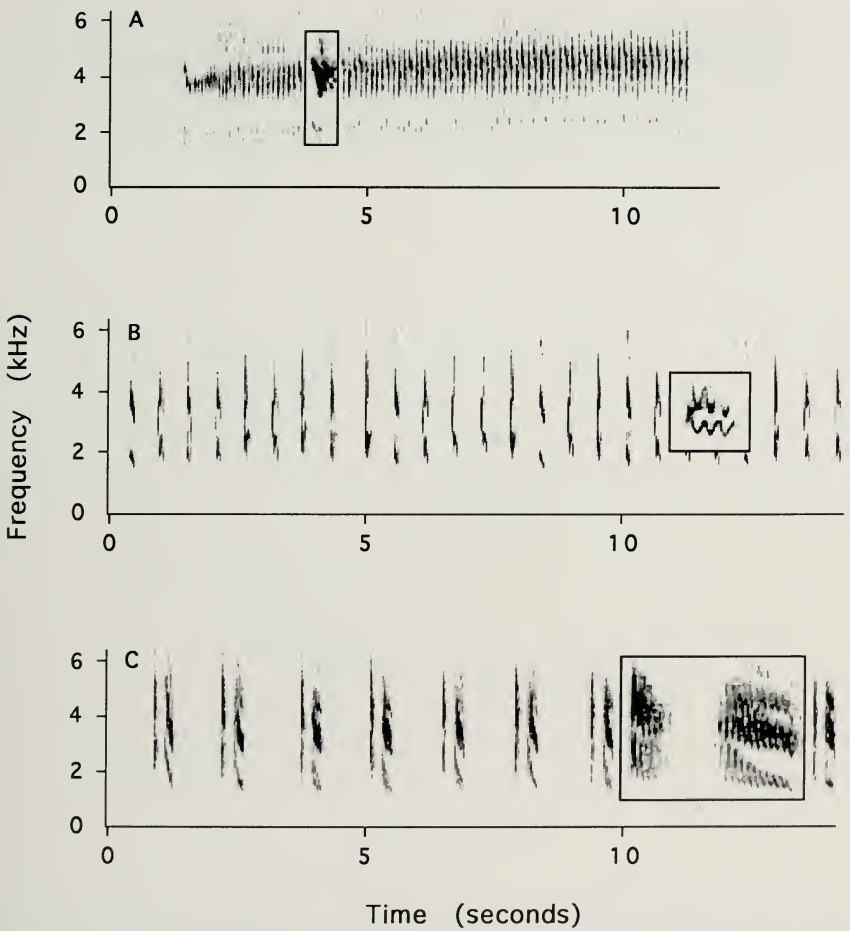

FIG. 4. Songs of other diademed/white-browed *Scytalopus*. A. *S. argentifrons*: age/sex unknown (male?), complete natural song. Costa Rica, Prov. Puntarenas, Monteverde Cloud Forest Preserve, 1600 m, 24 Mar 1983. B. Unnamed taxon: Adult male, natural(?) song; section of series of 45 continuous chirping notes; another series of 107 continuous notes also recorded; apparently neither was a truly complete series. Peru, Depto. Pasco, Millpo, approx. 3700 m, 29 July 1985; LSUMNS 128629; recorded by G. Rosenberg. C. *S. superciliaris* Adult male(?), section of song after playback, same as natural; length of series highly variable, from 27 notes, to 132 in 3:10 sec during a countersinging bout. Argentina, Prov. Tucumán, 13 km by road W Tafí del Valle, 2730 m, 20 Oct 1989.

last several minutes and often attracts other species of birds which may begin giving analogous vocalizations. When giving this vocalization, attention is directed at the observer, although the bird usually remains largely hidden from view. Individuals of all ages and both sexes of *S. schu-*

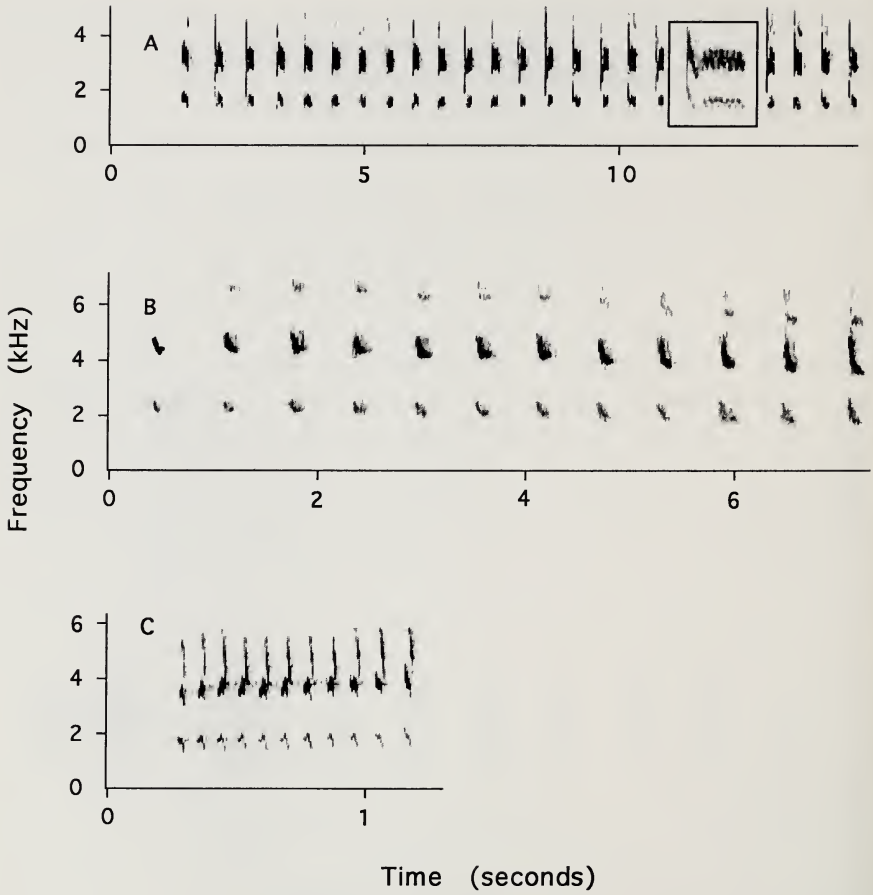

FIG. 5. Some vocalizations of *Scytalopus* [*magellanicus*] *acutirostris*. A. Adult (male ?), section of song after playback, same as natural. This song comprised 85 weakly bisyllabic notes, and lasted 50 sec. Depto. Cochabamba, Prov. Quillacollo, slopes of Cerro Tunari above Quillacollo, 3275 m, 14 Mar 1993. B. Subadult (age/sex unknown), natural descending series; number of notes variable from 4–12, often given by presumed female while male is singing. Same loc., 3400 m, 26 Feb 1992. C. Age/sex unknown, natural scold; this voc. not yet documented from Cochabamba populations. Depto. La Paz, Pongo, about 3615 m, 24 Mar 1992.

lenbergi give a version of this scold, with greater intra- than inter-individual variation displayed in the quality, pattern, frequency, and duration of scolds. Once an individual begins scolding/mobbing at regular intervals, however, scolds generally do not vary appreciably. Successive scolds of a single female (CBF No. 2629) soon after tape playback are

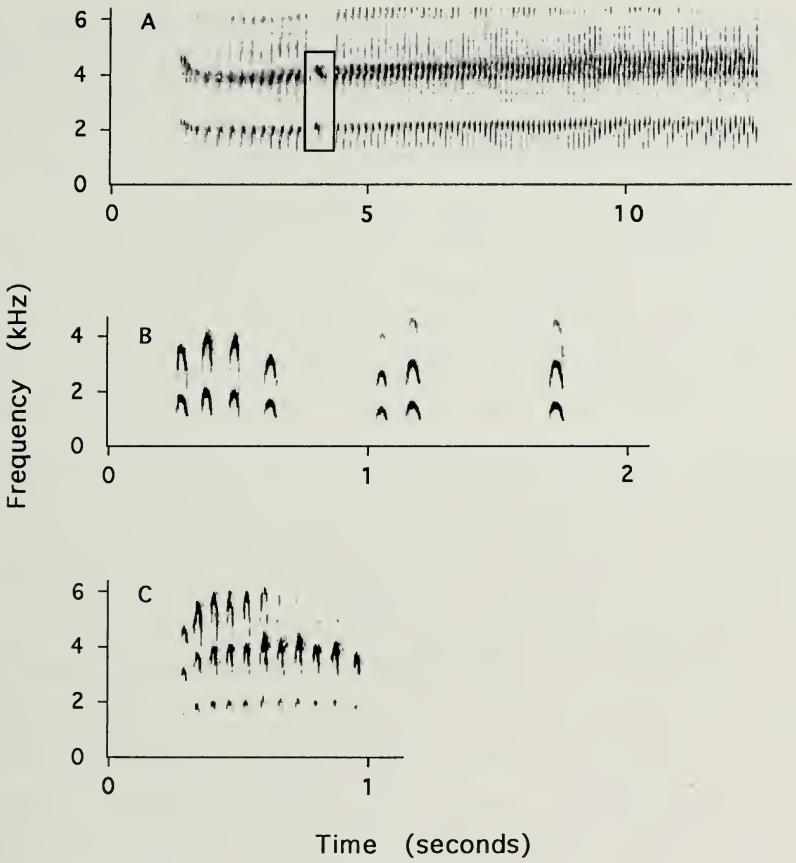

FIG. 6. Some vocalizations of *Scytalopus* '*unicolor*' *parvirostris*. A. Adult (male ?), complete natural song. Cochabamba, Prov. Chapare, 3 km by road E Tablas Monte, 2615 m, 27 Feb 1992. Same song is given by central La Paz and Santa Cruz populations; differs from that of populations in northern La Paz and southern Peru. B. Age/sex unknown, scold/mobbing vocalization in which 1–4 syllable phrases are alternated randomly but delivered at regular intervals. Same loc., 2535 m, 27 Feb 1992. C. Adult (sex unknown), natural scold. La Paz, Prov. Nor Yungas, about 1 km S Chuspipata, 3000 m, 28 Mar 1993; CBF 2635.

shown in Fig. 3D and E. The latter illustrates the scold most typical of the species, which this female began giving consistently several sec after I ceased tape playback. I suspect that females give the scold more often than do males and that females' scolds are slightly higher-pitched than those of males, as reported by Fjeldså and Krabbe (1990:423) for the genus in general. Across the genus *Scytalopus*, there is much less variation in scolds than in songs (pers. obs.; compare Fig. 3D and E with

probably distantly related but sympatric taxa in Figs. 5C and 6C). This probably indicates that the vocalizations we have identified as songs are more important than scolds as reproductive isolating mechanisms. There may be selective pressure to maintain (or converge toward) interspecific similarity of scolds/mobbing vocalizations if such lack of variation leads to widespread recognition of the warning or alert message among sympatric species of birds, as suggested by Thorpe (1956).

Other distinctive vocalizations of *S. schulenbergi* include a single, piercing "peeyk!" and an alarm call consisting of one or two sharp introductory notes followed by several level, evenly spaced couplets of sharp syllables, then a few triplets, ending with a higher syllable or two, the whole bout lasting 2–5 sec (N = 2). This vocalization is given only once, immediately after a bird is startled, as opposed to repeatedly like the scold.

Systematic relationships.—Looking for relatives among Andean *Scytalopus,* the conspicuous white forehead of *schulenbergi* immediately brings to mind the Andean Tapaculo (*S. magellanicus*) of Southern Argentina and Chile. However, the two have very different songs (compare Fig. 3A–C with sonagram p. 437 of Fjeldså and Krabbe [1990]) and, more importantly, there exists a near-continuum of populations (some unnamed) northward to central Peru (approximately the upper Huallaga River valley) sharing a *magellanicus*-type song, most of them essentially isolated geographically, and all occurring primarily at and above treeline. The entire range of *schulenbergi* (which inhabits humid-temperate forest at and below treeline) is paralleled by one of these forms, "*simonsi*" (sensu Fjeldså and Krabbe 1990), which lacks a conspicuous white forehead and has dark barring or other pattern on the flanks and rectrices in all plumages. In light of these considerations, I do not believe that *S. schulenbergi* can be assigned to the *magellanicus* superspecies (as defined below).

Perhaps with the exception of the taxa in eastern Brazil, the Silverfronted Tapaculo (*S. argentifrons*) of the mountains of Costa Rica and western Panama is the member of the genus most geographically remote from *S. schulenbergi.* The diademed adult male plumage (and to a lesser extent, the plumages of females and immatures) of *argentifrons* is, however, remarkably similar to that of *schulenbergi.* The basic pattern of the song of *argentifrons* (both subspecies) is also similar to that of *schulenbergi,* although it consistently begins more rapidly, and tends to rise slightly in frequency (Fig. 4A, compare with Fig. 3A and B). Scolds of the two species are also quite similar. It seems plausible that *argentifrons* and *schulenbergi* represent relicts at either end of an extraordinarily long, trans-Andean gap, although the gap could be occupied in part by taxa as

yet undiscovered. Such a relationship could easily be obscured, for example, if any extant, intervening relatives have lost the diadem or have not been tape-recorded. However, one intervening diademed population (only a small percentage of which have complete frontal bands) that has been tape-recorded, in western Depto. Pasco, Peru, is markedly different both by voice (a "chirping" note repeated at a short interval for long periods of time; Fjeldså and Krabbe 1990:440 and sonagrams pp. 437–442; [Fig. 4B, compare with Fig. 3A and B, Fig. 4A and C, and Fig. 5A]) and by habitat (above treeline in rocky shrub/grassland; G. and K. Rosenberg, pers. comm.). In both of these respects, the Pasco population appears to be most nearly allied to the *magellanicus* group. Although this distinctive population remains unnamed, it is almost certainly best treated as a species.

Particularly interesting is a series of four specimens taken within walking distance of a single camp at treeline in late July 1974 by T. A. Parker, III, D. A. Tallman, and G. Lester, 14 km NE of Abra Málaga along the road between Ollantaitambo and Quillabamba, Depto. Cuzco, Peru ("Canchaillo," 13°07′S, 72°22′W; Parker and O'Neill 1980). Habitat at this locality is heterogeneous, ranging from grassland with scattered rocks and shrubs to *Polylepis* woodland to dense, humid-temperate forest with abundant *Chusquea* spp. bamboo (Parker and O'Neill 1980). Two of the birds (LSUMNS No. 78578 [♂], 78581 [♀]) are very similar to *S.* [*m.*] *acutirostris* (this may actually be the appropriate name, but see comments below), and I suspect that they represent the *magellanicus* group occupying the grassland zone above treeline. One specimen's label gives the elevation as 13,000 ft (=about 3900 m) in *Polylepis* habitat, which, together with its plumage, places it almost certainly with the *magellanicus* group. The other specimen's label gives the elevation as "ca 10,700′ " (=3240 m), which, lacking precise data on habitat, makes its assignment to the *magellanicus* group somewhat more ambiguous. The other two specimens (LSUMNS No. 78579[♂], 78580[♀]) are distinctly diademed and masked and are basically quite similar to *schulenbergi*; I believe these birds represent an unnamed population. One specimen's label gives the elevation as "ca 10,700′," and the other's label gives no elevation; neither provides any data on habitat. If the *magellanicus*-like bird is indeed in the *Polylepis*/grassland habitats above treeline, as I believe it must be, I suspect that the unnamed, diademed taxon from below Abra Málaga is to be looked for in the somewhat isolated humid-temperate forest of this region, perhaps especially near the local treeline. A recording of the terminal part of a song made by N. Krabbe at "St. Luis restaurant below Abra Málaga, 3000 m. in *Chusquea* bamboo" on 4 Dec. 1983 (a "subadult," not described, was collected and is at ZMUC [no catalog number

provided], N. Krabbe, pers. comm.), and another recording of the end of a song followed by scolds recorded by T. Schulenberg "below Abra Málaga, 3350 m . . . in edge of humid forest," 21 Jul. 1985 (no specimen collected, N. Krabbe, pers. comm.) sound much like vocalizations of *schulenbergi.* Without specimens or even detailed plumage descriptions for either of the birds recorded, however, I must stop short of attributing these recordings to the diademed Abra Málaga population, especially in light of the following considerations. The two Abra Málaga specimens, which have well-developed diadems and masks and are probably adults, show extensive brownish flanks with some dark barring on most feathers, and have short, brown tails (averaging 4 mm shorter than the tail of *schulenbergi,* Table 1) with conspicuous, alternating light and dark concentric bands on the rectrices, in all these respects differing noticeably from *schulenbergi,* especially adults. Considering the substantial geographic hiatus between Abra Málaga and Valcón in Depto. Puno and these documented plumage and mensural differences (albeit from a sample of only two from Abra Málaga), and lacking a complete and unambiguous sample of the voice, I feel that the Abra Málaga population cannot be definitely allied to *schulenbergi* at the present, although I suspect that it is, whether at the specific or subspecific level.

The two distinctive, unnamed populations discussed here have escaped description primarily because they inhabit remote regions that had not been collected sufficiently or at all when Zimmer turned his attentions to the genus in the late '30s. Apparently, Zimmer never saw a diademed *Scytalopus* from the Andes, and although he described several subspecies from northern and central Peru (Zimmer 1939), he introduced no names that could be applicable to either of the taxa under consideration.

More recent interest in naming distinctive populations of *Scytalopus* in central Peru has been stymied to some extent by confusion surrounding the applicability of the name *acutirostris,* first associated with the *magellanicus* group by Hellmayr (Cory and Hellmayr 1924:21), because the type locality is not definitely known, and the type specimen is difficult to assign to any particular population (T. Schulenberg and N. Krabbe, pers. comm.). Fjeldså and Krabbe (1990:443) suggested that "*acutirostris*" may represent the same form as *S. unicolor parvirostris,* but, perhaps more likely, the 'unnamed' species from c. Peru" (which they discuss on pp. 427–428), but provided no explanation for this novel treatment. Not having examined pertinent type specimens myself, I am nonetheless impressed that Hellmayr was so convinced of the similarity between *S. m.* "*simonsi*" (from Cochabamba, Bolivia) and *acutirostris* (although he was not comparing types, I believe he had selected appropriate material for this specific comparison, because he had previously examined and criti-

cally described the type specimen of *acutirostris*) that he stated, "a small series from w. Bolivia . . . is perfectly identical with two from Maraynioc which we may regard as topotypical of *acutirostris*" (Cory and Hellmayr 1924:22). This similarity applies to the intervening Abra Málaga population of the *magellanicus* group as mentioned above, and strongly suggests that the traditional treatment of *acutirostris* in this assemblage is appropriate. In the absence of compelling evidence to the contrary, then, the most conservative course is to regard *acutirostris* as the species-level name representing the *magellanicus* complex occurring from central Junín, Peru, southward to central Cochabamba, Bolivia. I can see no clear reason to recognize "*simonsi*" (sensu Fjeldså and Krabbe 1990) at even the subspecies level. I agree with Fjeldså and Krabbe (1990) that this stretch of the Andes (Junín to Cochabamba) is probably inhabited by two or more allospecies in the *magellanicus* superspecies, and the name *simonsi* may stand for the population described from Cochabamba (whatever its distributional limits may be), but species limits in the *magellanicus* complex require further work to establish (perhaps involving analysis of "ancient DNA" to match the type of *acutirostris* to another central Peruvian population). Whether or not the above views are accepted, it seems clear that the name *acutirostris* cannot be applied to *schulenbergi,* nor to the diademed populations of *Scytalopus* inhabiting western Depto. Pasco or the Abra Málaga region in Depto. Cuzco.

Aside from the above considerations, I wish to point out that the population I have assigned to *S. schulenbergi* from Puno, Peru, really cannot be so designated with 100% certainty, because its song has not been tape-recorded. A recording made by N. Krabbe (pers. comm.) of the scold of an unseen *Scytalopus* "in fairly low, humid second growth above (N) Sandia, Puno, 2800 m on 25 Dec. 1983" sounds much like that of *S. schulenbergi,* although 2800 m is well below the elevation of any other specimen or recording of *schulenbergi,* including the LSUMNS series from Puno. Were it not for our discovery that *schulenbergi* definitely occurs within about 50 km (Pelechuco, in Depto. Franz Tamayo) with no reasonable geographic barrier in the intervening territory, I would be reluctant to include it because of the geographically complex gap southward to the type locality that would otherwise have to be included within the range. The known distribution of *S. schulenbergi,* from southern Puno, Peru, to Cochabamba, Bolivia, is shared by some other temperate-zone birds, such as *Andigena cucullata, Cranioleuca albiceps,* and *Hemispingus calophrys,* and it may be that these are its true limits.

The Bolivian range of *S. schulenbergi* may be fragmented by one or two natural barriers in Depto. La Paz: the canyons of the Rio La Paz and the Rio Mapiri, both of which represent arid or semi-arid gaps in the

distribution of humid-temperate forest on the east slope of the Andes. The former separates subspecies of at least three suboscines syntopic (pers. obs.) with *S. schulenbergi*: Black-throated Thistletail (*Schizoeaca harterti*) (Remsen 1981), Light-crowned Spinetail (*Cranioleuca albiceps*) (Remsen 1984), and *Grallaria rufula.* The Rio Mapiri canyon appears to be the most likely barrier separating *Schizoeaca harterti* and *S. helleri.* Thus, further investigation within Bolivia, especially in Depto. Cochabamba, may reveal that *S. schulenbergi* comprises two or three subspecies.

Biochemical analysis using specimens of known elevation and habitat and with accompanying voice recordings, including *S. schulenbergi,* currently is underway at ZMUC by P. Arctander (J. Fjeldså, in litt.).

Conservation.—For the present, *S. schulenbergi* is probably not seriously threatened as humid-temperate forest between 3100 and 3400 m exists in undisturbed condition in several remote regions of its range. The type locality, however, has been altered significantly in the past two years by the activities of a gold-mining cooperative which has encouraged more than 500 people to settle in a formerly pristine, forested canyon there. Fortunately, the Bolivian government has established and is planning to designate some important reserves that will protect not only taxa with distributions largely within Bolivia, such as *S. schulenbergi,* but also genetic corridors for the many more taxa that extend significantly north or south of the country.

Distribution and vocalizations of other Bolivian Scytalopus, *with comments on the* magellanicus *complex.*—From central Depto. Cochabamba northward to the Peruvian border, four taxa of *Scytalopus* are found as one descends from rocky grassland above treeline to the upper tropical rain forest of the east slope, in the following sequence: [*m.*] *acutirostris*; *schulenbergi*; '*unicolor*' *parvirostris*; and '*femoralis*' *bolivianus.* These four taxa may be encountered within a 20 km drive along the road between Unduavi and Coroico in Depto. La Paz. The situation south of central Depto. Cochabamba is much simpler, with the depression of treeline and lower rainfall significantly narrowing the elevational width of humid forest. In this region, the first two taxa above drop out, *S.* [*m.*] *superciliaris* appears (perhaps as far north as central Depto. Cochabamba; see below), continuing southward to Prov. Tucumán, Argentina, and *S.* '*unicolor*' *parvirostris* reaches its southernmost point of occurrence in extreme western Depto. Santa Cruz in the isolated Serrania de Siberia (Remsen and Traylor 1989, pers. obs.). In lower subtropical and upper tropical forests, *S.* '*femoralis*' *bolivianus* is reported in the literature as far south as Prov. Florida, Depto. Santa Cruz (Remsen et al. 1986), and it has been found recently in Depto. Chuquisaca by J. Fjeldså and S. Maijer (J. Fjeldså, pers. comm.). Thus, only *S.* [*m.*] *superciliaris zimmeri*

is known to inhabit most of the southern half of Bolivia, especially at upper elevations. Songs and habitats of all these forms, with the exception of *S.* [*m.*] *superciliaris,* are at least partially described and illustrated with sonagrams in Fjeldså and Krabbe (1990). I offer the following information to supplement their species accounts, with emphasis on *Scytalopus* taxa within Bolivia, concluding with comments on the *magellanicus* complex.

S. 'unicolor' parvirostris.—In Bolivia, this taxon inhabits well-developed humid montane forest and connected second-growth and bamboo between about 2000 and 3200 m. It overlaps *S. 'femoralis' bolivianus* at the lower end, between about 2000 and 2300 m (but see account of *bolivianus* below), and *S. schulenbergi* at the upper end, between about 2975 and 3100 m. A full song from Prov. Chapare, Cochabamba is shown in Fig. 6A. Birds to the south in Depto. Santa Cruz, and those to the north, near the type locality of *parvirostris* in Depto. La Paz, have songs essentially indistinguishable from those of Cochabamba birds (pers. obs.). The population inhabiting the Pelechuco region of Prov. Franz Tamayo, however, sings a markedly different song. Although I did not manage to tape record it, I believe this song, which is characterized by significantly longer inter-syllable interval and is of a distinctive quality, is represented by the partial sonagram labeled "*parvirostris* Vilcabamba mts. (song)" on p. 426 of Fjeldså and Krabbe (1990), who described some variation in songs within the latitudinal range they ascribe to *parvirostris* (p. 427). No songs of topotypical *parvirostris* were heard during two days in appropriate habitat at proper elevations. Playback experiments that I performed by presenting songs of topotypical *parvirostris* to the birds below Pelechuco elicited no response, but scolds of this taxon from Prov. Nor Yungas and of *S. schulenbergi* caused previously undetected individuals to vocalize, once with a song, and once with a scold. A single female was collected (CBF No. 2646), which differs from a single female from Prov. Nor Yungas (essentially topotypical *parvirostris*) in having slightly more brown in the upper back and nuchal region, and somewhat less rufous-brown in the flanks (differences that I suspect comparison of series would show to be inconsistent). I was not able to perform reverse playback experiments. These two distinct song types apparently replace each other somewhere in northern Bolivia, perhaps across the Rio Mapiri. Further elucidation of this interesting situation awaits more field and biochemical work.

Two types of repetitive scold/mobbing vocalizations are illustrated in Fig. 6B and C. These are given by individuals from central La Paz southward at least to Santa Cruz. Both seem to stimulate other birds to scold as well. I do not know the difference in context in which these scolds are

given, except that I have noted that the scold in Fig. 6C seems to be given more frequently in response to the presence of an observer.

S. 'femoralis' bolivianus.—This little-known taxon primarily inhabits the interior of tall forest, favoring ravines and dark tangles at the edge of light gaps. It is frequently heard in the dense, herbaceous vegetation along roads in generally forested regions, mostly between about 1100 and 2300 m (pers. obs.). *S.* '*femoralis*' *bolivianus* has an extensive vocal repertoire, including variation in inter-syllable interval of the songs given by a single individual (particularly apparent following tape playback). Part of a typical song, which does not include the beginning, is shown in the sonagram on p. 431 of Fjeldså and Krabbe (1990). The scold consists of fewer syllables than the scolds of other Bolivian *Scytalopus,* but is structured similarly. I have one anomalous record of an individual that I heard singing at the remarkably high elevation of 2850 m below Pelechuco in Prov. Franz Tamayo. Elsewhere in the northern half of Bolivia, only '*unicolor*' *parvirostris* is known to occur at this elevation. In the Pelechuco region, however, true *parvirostris* appears to be replaced by another taxon (see above). Further investigation could show this taxon to have a somewhat different elevational distribution, or perhaps '*femoralis*' *bolivianus* truly occupies a wider elevational range in this part of Bolivia.

S. [m.] superciliaris.—A typical section of the long song of *superciliaris,* in which it delivers a labored series of conspicuously bisyllabic notes in the pattern of nominate *magellanicus* to the south (see sonagram p. 437 of Fjeldså and Krabbe 1990), and [*m.*] *acutirostris* to the north (Fig. 5A), is shown in Fig. 4C. Nominate *superciliaris* lives in a wide variety of habitats, from dry, rocky ravines well above treeline where the dominant vegetation is *Festuca* sp. grass to rocky ravines and talus slopes in the much more humid *Alnus* and "yungas" forests as low as about 1400 m (pers. obs.). The subspecies *zimmeri,* known to occur only in Deptos. Chuquisaca and Tarija, "sounds like a *superciliaris,* but has the stress on first instead of second syllable" (recording by J Fjeldså, N. Krabbe, pers. comm.). Both by voice and by plumage, N. Krabbe (pers. comm.) considers *zimmeri* to be intermediate between nominate *superciliaris* to the south and "*simonsi*" to the north, and favors merging the three forms under *superciliaris* (the oldest name).

A female (LSUMNS 37781) collected by Steinbach in October 1937 at Colomi in the mountains of central Cochabamba (17°21′S, 65°52′W, 3800 m; Paynter 1992) may represent an intergrade between *zimmeri* and *acutirostris*/"*simonsi.*" It has a distinct white superciliary narrowly crossing the forehead, and thick, dark bars on the rump, flanks, tail coverts, and tail. The throat is slightly paler gray than the breast. Two additional intergrades were collected in 1987 at "Khasa Punta Pampa near Rodeo

W of Vacas, Cochabamba (DNA analyzed)" (J. Fjeldså, pers. comm.). That *zimmeri* and *acutirostris*/"*simonsi*" might hybridize is not surprising given the lack of an obvious geographic barrier, the fact that they at least partially share the same habitat, and the relatively close similarity in their songs. I expect that these two or other "species" of *Scytalopus* occasionally interbreed, because many populations of *Scytalopus* (named or not) are in direct contact with at least one other morphologically similar population, and this circumstance is compounded by the crowding effect resulting from human alteration of natural habitats: different vocalizations and habitats may not always ensure reproductive isolation. The lack of external structural and plumage differentiation across the genus must also make it very difficult or impossible for researchers to recognize a hybrid individual in the vast majority of instances. However, under those relatively rare circumstances in which one finds two vocally and morphologically similar but separable populations in geographical proximity, such as the *magellanicus* form in central Cochabamba (whether correctly called *acutirostris* or "*simonsi*") and *superciliaris zimmeri,* recognition of a hybrid should be comparatively easy.

S. [m.] acutirostris.—This taxon (which may properly be known as *simonsi*; see above) inhabits rocky shrub/grassland above natural treeline. It has a rather extensive vocal repertoire, including several characteristic one- and two-note vocalizations that appear to function as alarm or pair contact calls, and several vocalizations given mostly in response to tape playback. After the song (Fig. 5A), the most commonly heard vocalization is a descending, slightly accelerating series of "weenk" notes delivered slowly enough to be counted easily (Fig. 5B). Similar kinds of vocalizations are given by the huge *Pteroptochos* tapaculos in Chile (pers. obs.). This vocalization is certainly given by females (CBF No. 2642), often while the male is singing, and it may be given by males as well. In any event, it is delivered only once, and at irregular intervals. The scold in Depto. La Paz is shown in Fig. 5C. I am perplexed by the fact that I have not heard this scold (or any "substitute" scold) from birds in Depto. Cochabamba, although I have encountered many individuals in several localities there.

The "*magellanicus* group/complex," first defined in Zimmer's (1939) strictly morphological classification, comprises "the smallest and at the same time elevationally highest-ranging members of the genus," including taxa from northwestern Venezuela south to Tierra del Fuego and the Cape Horn Archipelago (Fjeldså and Krabbe 1990:437–443). These many forms are currently treated (with the single exception of *superciliaris*) either as a single species with numerous subspecies (Sibley and Monroe 1990) or as allospecies of a single superspecies (Fjeldså and Krabbe 1990:

437). There is, however, a clear break in song-types and, to a lesser extent, habitats, within this assemblage at the "North Peruvian Low" (defined by Vuilleumier 1984) in Depto. Cajamarca, northwestern Peru (pers. obs.). Populations to the south of this barrier have songs that are a long series (occasionally in excess of 3 min) of steadily cadenced, monosyllabic or bisyllabic notes (these occur from approximately the upper Huallaga River valley southward to Cape Horn; Fjeldså and Krabbe 1990, sonagrams pp. 437, 439, 440, top of 441; pers. obs.). In a few forms this pattern is varied to a long series of short, burry notes (Fjeldså and Krabbe 1990, sonagrams pp. 437, bottom of 441, and top of 442; pers. obs.). Populations to the north of the North Peruvian Low for which voices are known have songs that consist of a single, vibrating trill several seconds long (perhaps averaging 10–15 sec), in which individual syllables are delivered at a rate of more than 30/sec, and which, in the taxon *griseicollis,* often begin with 1–3 short stutters, then continue without interruption, slowing slightly toward the end (pers. obs.). There are two anomalies to this scenario: Hilty and Brown (1986:429) attributed a vocalization transcribed as "a measured ser. of double whistles, ty-ook, ty-ook, ty-ook . . ." to *S.* '*magellanicus*' *canus* in Depto. Nariño, Colombia, and Fjeldså and Krabbe (1990:442) suggested that birds from Cerro Chinguela, Depto. Piura (north of the North Peruvian Low), may represent *S.* [*m.*] *affinis,* which otherwise occurs only to the south of the North Peruvian Low, and which sings a southern song type (sonagram p. 442). N. Krabbe considers the song of *canus* unknown (pers. comm., contra Fjeldså and Krabbe 1990:443), and my field experience indicates that the "*magellanicus*" population high on Cerro Chinguela sings a northern song type, which is apparently the same as that of *S.* '*magellanicus*' *opacus* of Ecuador, the nearest form to the north. Additionally, it seems that northern populations tend to favor woody vegetation and bamboo along the forest/páramo ecotone more than the relatively open, rocky shrub/grassland inhabited by most of the southern populations. Therefore, I recommend that the *magellanicus* complex be reorganized to allow these two high-altitude, geographically isolated, vocally distinct groups to stand on their own as superspecies, maintaining the name *magellanicus* for populations south of the North Peruvian Low that are vocally and genetically determined to be allied to nominate *magellanicus* (I suspect that there is more than one group within the southern assemblage) and establishing the name *griseicollis* for vocally and genetically related populations north of the North Peruvian Low. Inherent in this reorganization is the reinstatement of *griseicollis* to species status. Species limits within these superspecies, and the degree of relatedness of the two superspecies themselves, will require

further field and laboratory work to determine and, in any case, are beyond the scope of this paper.

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COLOR PLATE

The frontispiece painting by Jon Fjeldså has been made possible by an endowment established by George Miksch Sutton.

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DEMOGRAPHY AND MOVEMENTS OF THE ENDANGERED AKEPA AND HAWAII CREEPER

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Abstract.—We studied populations of the endangered Akepa (*Loxops coccineus coccineus*) and Hawaii Creeper (*Oreomystis mana*) at four sites on the island of Hawaii. Mean monthly density (±SE) of Akepa was 5.74 ± 0.87, 1.35 ± 0.41, 0.96 ± 0.13, and 0.76 ± 0.12 Akepa/ha at Kau Forest, Hamakua, Keauhou Ranch, and Kilauea Forest study areas, respectively. Hawaii Creepers were found at densities of 1.68 ± 0.53, 1.79 ± 0.42, 0.48 ± 0.06, and 0.54 ± 0.08 birds/ha, respectively, at the four study areas. Highest capture rates and numbers of birds counted from stations occurred from August through November and February through March. Hatching-year birds were captured from May through December for Akepa and April through December for Hawaii Creeper. Annual survival for adults at Keauhou Ranch was 0.70 ± 0.27 SE for 61 Akepa and 0.73 ± 0.12 SE for 49 Hawaii Creepers. Lowest rates of mortality and emigration occurred between May and August. Both species appeared to defend Type-B territories typical of cardueline finches, retained mates for more than one year, and showed strong philopatry. Home ranges for Hawaii Creepers ($\bar{x}$ = 7.48 ha) were larger than those for Akepa ($\bar{x}$ = 3.94 ha). No difference was found between home range sizes of males and females for either species. *Received 21 Dec. 1993, accepted 20 April 1994.*

The Hawaii subspecies of the Akepa (*Loxops coccineus coccineus*) and the Hawaii Creeper (*Oreomystis mana*) are endangered Hawaiian honeycreepers (Fringillidae: Drepanidinae) found only in wet and mesic forests above 1000 m elevation on the island of Hawaii. The two species are similar in that they are insectivorous and occur at highest densities in native forests of ohia (*Metrosideros polymorpha*) and koa (*Acacia koa*) where they are mostly syntopic (Scott et al. 1986). Both species have extended breeding and molting periods that reflect the low degree of seasonality in their food supply and environment (Ralph and Fancy 1994a). Because they live in dense, remote rainforests, usually in low density, little is known about the life history of either species.

The Akepa on Hawaii occurs in four disjunct populations totaling 14,000 birds, with highest densities in subalpine ohia woodland in the Kau Forest Reserve (Scott et al. 1986, Pratt et al. 1989). Akepa were once abundant and widely distributed on Hawaii (Perkins 1903). Pratt (1991) considered the Akekee on Kauai to be a separate species (*L. caeruleirostris*) and suggested that the very rare Maui and Oahu forms of Akepa may warrant recognition as full species. Akepa have unusual bills with crossed mandibles which they use to extract spiders and other invertebrate prey from ohia

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terminal buds; they also glean insects from foliage (Perkins 1903, Mueller-Dombois et al. 1981b, Ralph and Noon 1986, Ralph 1990). The Akepa on Hawaii appears to be an obligate cavity nester (Freed et al. 1987).

Scott et al. (1986) found four widely separated populations of Hawaii Creepers on Hawaii and estimated the total population at 12,500 birds. Highest densities occurred between 1500 and 1900 m elevation in relatively undisturbed forests in the Kau Forest Reserve and on the eastern slope of Mauna Kea and the northeastern slope of Mauna Loa (Scott et al. 1986). Perkins (1903) reported that *O. mana* was "a very abundant bird and generally distributed over the large island," although he noted distributional anomalies in forests of the middle Kona and Puna districts. Hawaii Creepers feed primarily by bark gleaning on larger stems and branches of trees, whereas Akepa are predominately foliage gleaners that use the perimeters of tree crowns (Mueller-Dombois et al. 1981b).

In this paper, we present findings from a field study of Hawaii Creepers and Akepa which was part of a research program on foraging ecology and population dynamics of Hawaiian forest birds conducted by the U.S. Forest Service 1976–1982.

STUDY AREAS AND METHODS

We studied Hawaii Creepers and Akepa at four sites on the island of Hawaii between November 1976 and January 1982. The Keauhou Ranch study area (19°30′N, 155°20′W; 1800 m elevation) had a discontinuous canopy dominated by ohia and naio (*Myoporum sandwicense*) and had a long history of grazing by cattle and logging for koa and ohia. A 16-ha grid marked at 50-m intervals was established at this wet (ca 2000 mm annual rainfall) forest site. The 16-ha Kilauea Forest study area (19°31′N, 155°19′W; 1600–1650 m) was in a relatively pristine, closed-canopy, wet forest dominated by 20–30 m tall koa and 15–25 m tall ohia trees, and was approximately 1.8 km NW of the Keauhou Ranch study area. This site was described in detail by Mueller-Dombois et al. (1981a:216–220). The 50-ha Hamakua study area near Pua Akala (19°47′N, 155°20′W; 1770 m) was similar to the Keauhou Ranch site but had a more continuous canopy and an almost complete lack of native understory plants because of intensive grazing by cattle. The 50-ha Kau Forest study area (19°13′N, 155°39′W; 1750 m) had a closed canopy of ohia and a largely ungrazed understory of kolea (*Myrsine lessertiana*), olapa (*Cheirodendron trigynum*), kawau (*Ilex anomala*), and native ferns.

We estimated densities of Hawaii Creepers and Akepa at each of the four study areas by the variable circular-plot method (Reynolds et al. 1980, Ramsey and Scott 1979) during eight-min count periods as described in Ralph (1981). All observers were trained extensively to identify birds by songs and calls and to estimate distances to birds (Kepler and Scott 1981). At the Keauhou Ranch and Kilauea Forest sites, we established 25 count stations at 100-m intervals on a square, 16-ha grid, and attempted to count birds at each site three times each month (Table 1). At the Hamakua and Kau Forest sites, we counted birds at approximately four-month intervals during 1979–1980 from 15 stations spaced at 100-m intervals along U-shaped transects. Data were analyzed with the program VCP2 (E. Garton, unpubl. data), which calculates bird densities from data collected by the variable circular-plot method. Paired *t*-tests were used to compare densities between Akepa and Hawaii Creepers within each of the four study areas.

TABLE 1
NUMBER OF EIGHT-MIN COUNT PERIODS CENSUSED

Year	Study area	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1977	Keauhou Ranch							25	25	25	25	25	25
1978	Keauhou Ranch	25	25	50	50	75	75	62	75	76	62	75	51
	Kilauea Forest				50	49	50	75	75	85	85	75	44
1979	Keauhou Ranch	75	75	81	100	75	101	75	72	78	76	87	87
	Kilauea Forest	40	74	50	87	75	75	75	75	75	75	75	
	Hamakua		45			30			45				40
	Kau Forest						45			45			
1980	Keauhou Ranch	96	88	76	87	125	75	73	75	99	26	63	49
	Kilauea Forest		162			142			150		75	50	
	Hamakua			15	15		36		45				38
	Kau Forest	45			45			40			45		40
1981	Keauhou Ranch	84	75	100	50	75	75	74	75	75	75	75	75
	Kilauea Forest	63	87										
1982	Keauhou Ranch	62											

We captured birds in mist nets at two of our study areas, Keauhou Ranch (N = 62,006 net-h) and Kilauea Forest (N = 16,958 net-h) and conducted monthly surveys to search for color-banded birds. We regularly operated nets at 16 permanent sites and placed 10 additional nets at other locations throughout the grids as personnel were available. We operated a net within 75 m of every point in each study site at least once every three months. Captured birds were banded with USFWS bands and a unique combination of three colored plastic bands. Each bird was inspected to determine molt status and presence or absence of a brood patch or enlarged cloacal protuberance (Pyle et al. 1987, Ralph et al. 1993). Sex was determined by plumage characteristics or presence of a brood patch or cloacal protuberance, or for a few individuals, by observations of breeding behavior during subsequent monthly surveys. We identified HY birds on the basis of plumage characteristics, skull ossification, and behavior.

At least monthly, we conducted surveys at Keauhou Ranch and Kilauea Forest to identify and record activities of color-banded birds (Ralph and Fancy 1994a). We noted the presence, and where possible, identified any birds associated with the focal bird. The date and location of individuals identified during these surveys were used in conjunction with banding records to calculate survival rates and home range size.

We estimated annual survival of Akepa and Hawaii Creepers from capture-recapture (including resightings) data with the Jolly-Seber model (Pollock et al. 1990). The Jolly-Seber method is superior to those equating survival with recapture rates because the model explicitly allows for the possibility that an individual is alive and in the study area but is not observed (Nichols and Pollock 1983). Annual survival (the complement of which includes both mortality and permanent emigration from the study area) was calculated with Model AX of program JOLLY (Pollock et al. 1990) which incorporates data from resightings and allows for time-specific capture and survival probabilities. We selected a series of four-month sampling periods from January through April of each year during 1977–1981 based on goodness of fit tests from preliminary runs. All birds captured or resighted during the eight-month period from May through December were coded as resightings (Pollock et al. 1990:85).

We recorded locations of individuals captured in nets or identified during surveys to the

nearest 50 m within an expanded 600 × 600 m grid at the Keauhou Ranch and Kilauea Forest sites. Bird locations and associated attribute data (e.g., date, sex, and age of individual) were analyzed with a geographic information system to determine the extent of overlap among individuals. Differences between species and age classes in the length of time that individuals were observed at Keauhou Ranch were tested by two-way ANOVA. Home ranges were calculated by the minimum convex polygon method (Mohr 1947, Hayne 1949). For each individual, we also calculated the median distance from the bird's center of activity to each location where it was observed (Hayne 1949, Fancy et al. 1993). We compared home range size and distance from the center of activity between sexes and species by two-way ANOVA. After inspecting plots of home range size versus sample size, we excluded individuals observed at <10 locations from further analysis because of biases associated with small sample sizes (Bekoff and Mech 1984, Swihart and Slade 1985).

RESULTS

Density and capture rates.—Mean monthly density (birds/ha) of Akepa for all months combined was 0.96 ± 0.13 SE at Keauhou Ranch, 0.76 ± 0.12 at Kilauea Forest, 1.35 ± 0.41 at Hamakua, and 5.74 ± 0.87 at Kau Forest, respectively. Hawaii Creepers were found at mean densities of 1.68 ± 0.53, 1.79 ± 0.42, 0.48 ± 0.06, and 0.54 ± 0.08 birds/ha, respectively, at the four study areas. Densities of Akepa at Kau Forest were higher than those for the other three sites (Tukey's test, df = 97, $P < 0.05$) which did not differ from each other. Densities of Hawaii Creeper did not differ between Kau Forest and Hamakua nor between Keauhou Ranch and Kilauea Forest, but densities at Kau Forest and Hamakua were both greater than those at the other two sites (Tukey's test, df = 97, $P < 0.05$).

At all sites except Kau Forest, we observed a post-breeding increase in the Akepa population during late summer or fall each year (Figs. 1–4). Seasonal changes in densities of Hawaii Creepers were less pronounced than those for Akepa, and the timing of post-breeding peaks was inconsistent among study areas (Figs. 1–4). Densities of Akepa were higher than those of Hawaii Creepers at Keauhou Ranch (. = 4.51, df = 54, P = 0.0001) and Kau Forest (t = 8.68, df = 7, P = 0.0001) but not at Kilauea Forest (t = 1.51, df = 28, P = 0.14) or Hamakua (t = 0.81, df = 8, P = 0.44).

Monthly capture rates (Fig. 5) were correlated with mean monthly densities (all years combined) for both Akepa (r = 0.64, P = 0.02) and Hawaii Creepers (r = 0.62, P = 0.03). Highest capture rates occurred during August through November and in February and March for Akepa, and during October through March for Hawaii Creeper. We captured HY Akepa from May through December, with a peak in August through October, and HY Hawaii Creepers from April through December, with a peak in August through November (Fig. 5).

Annual survival.—We calculated survival probability for Akepa and Hawaii Creepers at only the Keauhou Ranch site because we mist netted at

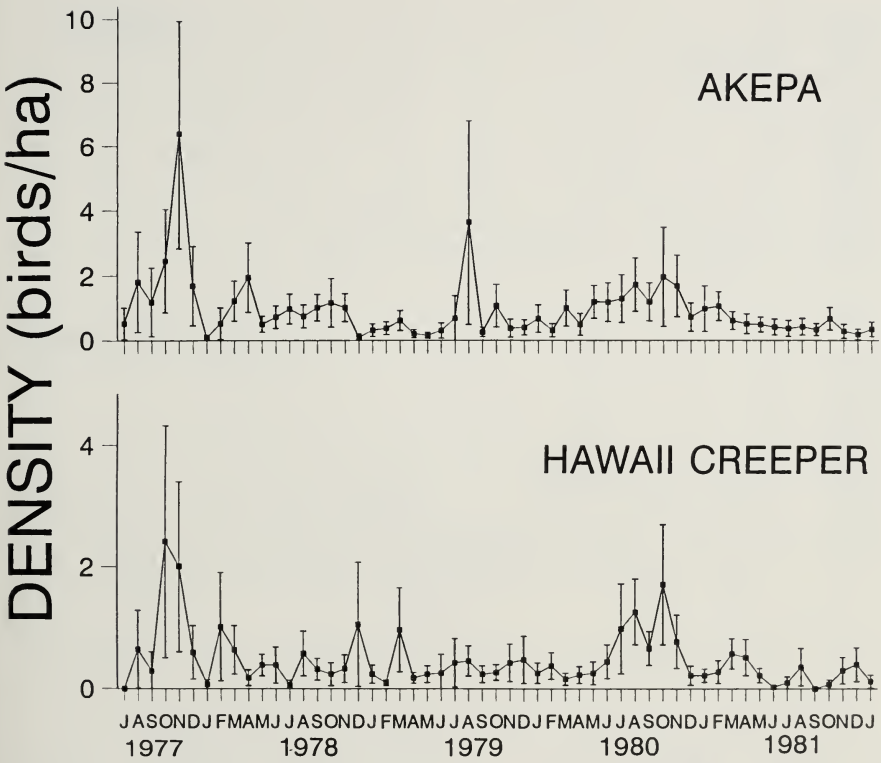

FIG. 1. Mean density (birds/ha, ± 1 SE) of Akepa and Hawaii Creeper at Keauhou Ranch.

Kilauea Forest for only two years. Capture and resighting data for birds first captured as HY birds was inadequate to fit an age-specific model, but we were able to calculate survival of adults (after hatching year, AHY). Fifteen of the 30 HY Akepa we captured at Keauhou Ranch were never seen again, and six of the remaining HY Akepa were last seen within six months of their initial capture. Only seven of the 30 (23%) HY Akepa were alive and still in the study area after one year. Twenty Hawaii Creeper were first captured as HY birds at Keauhou Ranch; 10 of these were never seen again, two were last seen within six months of their initial capture, and eight (40%) were still in the study area one year later.

Mean annual survival for AHY Akepa, based on 442 records of 61 birds at Keauhou Ranch, was 0.70 ± 0.27. The probability of resighting an individual in a given year if that individual was alive and in the study area was 0.60 ± 0.22. Similar calculations for 493 captures and resightings of

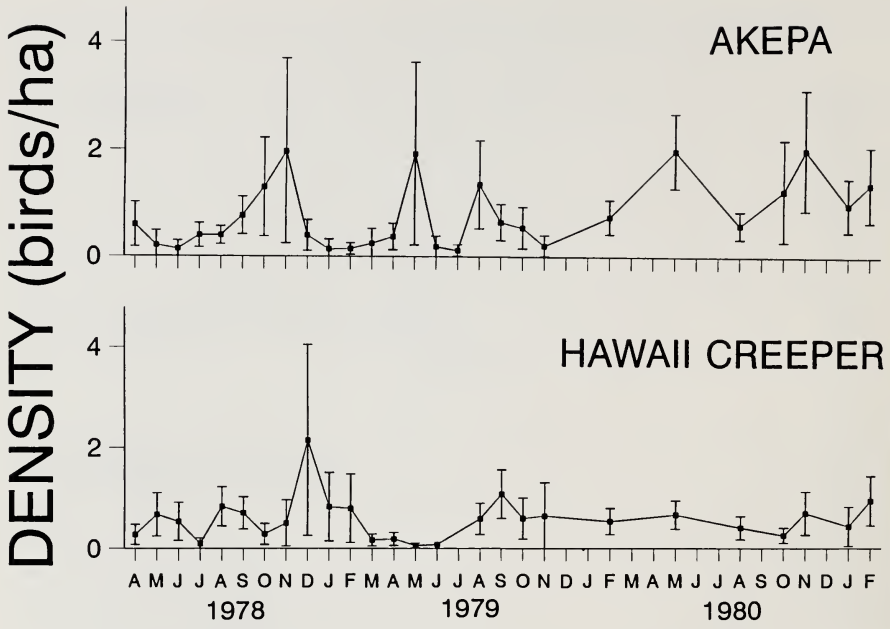

FIG. 2. Mean density (birds/ha, ± 1 SE) of Akepa and Hawaii Creeper at Kilauea Forest.

49 Hawaii Creepers yielded an estimated survival probability of 0.73 ± 0.12, with a resighting probability of 0.73 ± 0.26. Most birds observed for a minimum of two months were last observed during the winter, between September and March, in both species. Lowest rates of mortality or emigration occurred between May and August.

Philopatry and movements.—We observed Akepa and Hawaii Creepers with the same mates in more than one year, and many individuals showed strong philopatry. For example, one male Akepa remained at the Keauhou Ranch site from March 1977 until the end of the study in January 1982. He was frequently observed with a female that was captured in February 1978 and last seen in January 1981. Another Akepa pair, both captured in July 1977, remained together at Keauhou Ranch until February 1979 when the female disappeared. A pair of Hawaii Creepers that were captured together on 16 March 1977 and fledged a chick at the Keauhou Ranch site in April remained together at the study site through July 1978, after which the male disappeared. We never noted any case of mate switching in either species.

We found differences in philopatry between species and age classes (Table 2). The mean number of months that Hawaii Creepers (N = 10 HY,

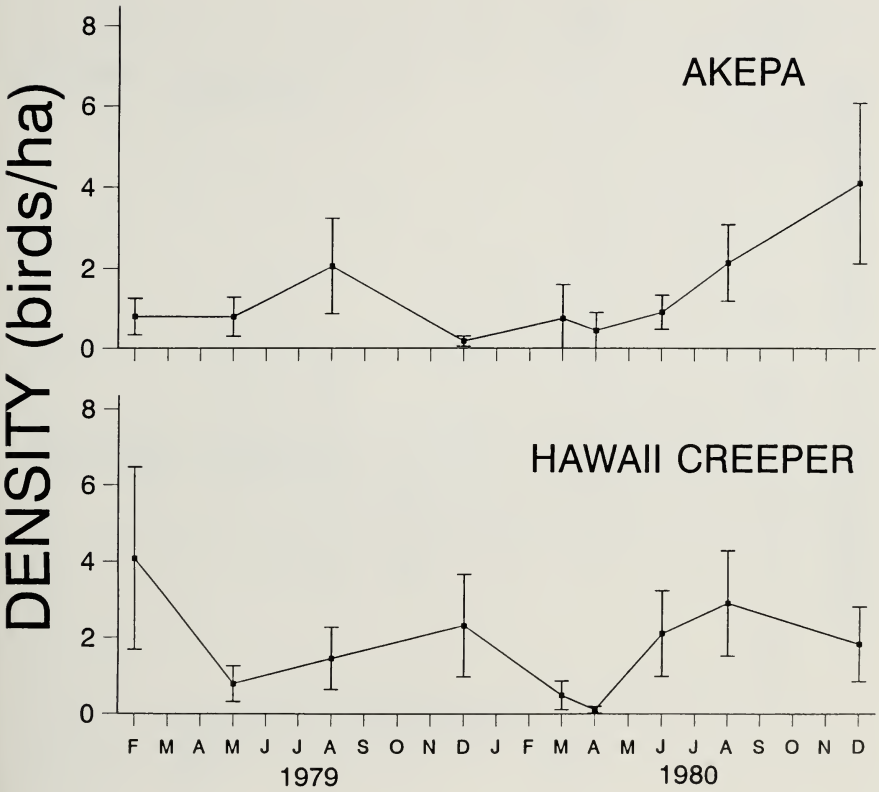

FIG. 3. Mean density (birds/ha, ± 1 SE) of Akepa and Hawaii Creeper at Hamakua.

29 AHY) remained at the Keauhou Ranch site was greater than that for Akepa (N = 15 HY, 33 AHY; $F = 7.86$, $P = 0.006$), and birds first captured as AHY birds remained longer than did HY birds ($F = 4.95$, $P = 0.028$). Considering only AHY birds, 19 of 52 (36.5%) Akepa were seen only once on the study area, compared to nine of 38 (23.6%) Hawaii Creepers.

Home ranges of Akepa and Hawaii Creeper overlapped extensively with other individuals of the same species, and neither species appeared to defend Type-A territories (Nice 1941). Plots of locations where breeding pairs of Akepa and Hawaii Creepers were observed during the peak breeding season of March through June (Ralph and Fancy 1994a) showed overlap among pairs and occurrence of one or more unpaired males within each pair's home range. Home range size of individuals with ≥10 locations was highly correlated with distance from the center of activity for both species

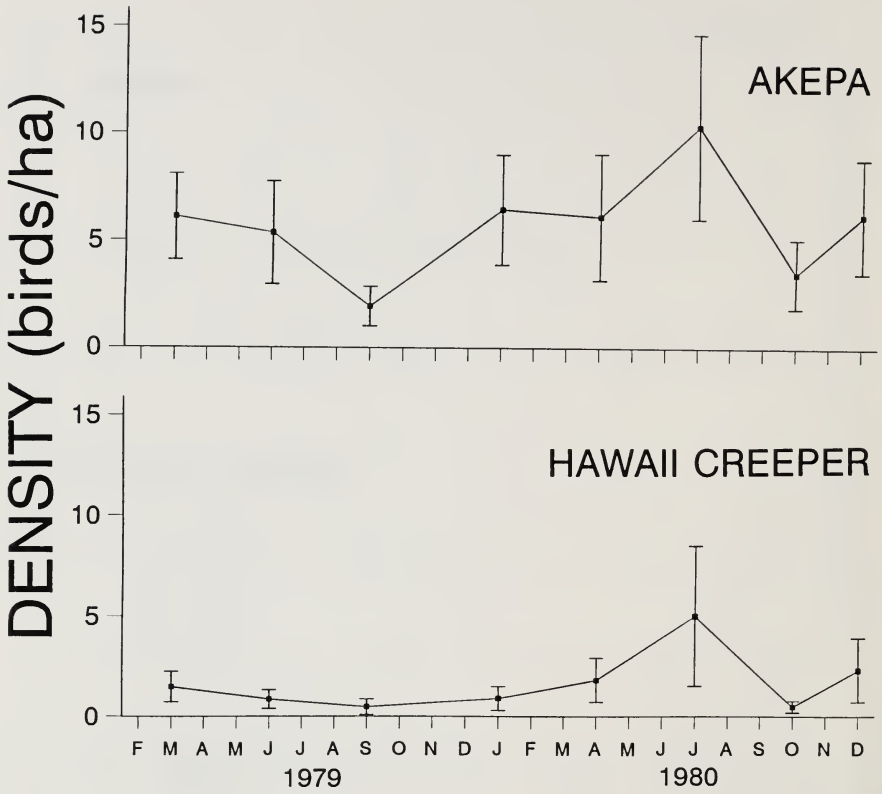

FIG. 4. Mean density (birds/ha, ± 1 SE) of Akepa and Hawaii Creeper at Kau Forest.

(r = 0.76, N = 18, P = 0.0002 for Akepa; r = 0.67, N = 20, P = 0.0012 for Hawaii Creepers), and statistical tests were always in agreement for the two measures. We found no difference in home range size (F = 0.37, P = 0.55) or median distance (F = 0.33, P = 0.57) between males and females of either species (Table 3). Home range size for Hawaii Creepers ($\bar{x}$ = 7.48 ha, N = 20, data for both sexes combined) was significantly greater than that for Akepa ($\bar{x}$ = 3.94 ha, N = 18, F = 9.42, P = 0.0045).

DISCUSSION

We found highest densities of Akepa and Hawaii Creepers at the Kau Forest and Hamakua study areas, as did Scott et al. (1986) during the Hawaiian Forest Bird Surveys. Mean Akepa density in the Kau Forest was 5–6 times higher than those estimated for the Keauhou Ranch and Kilauea Forest sites. Hawaii Creepers were most common at the Hamakua and Kau

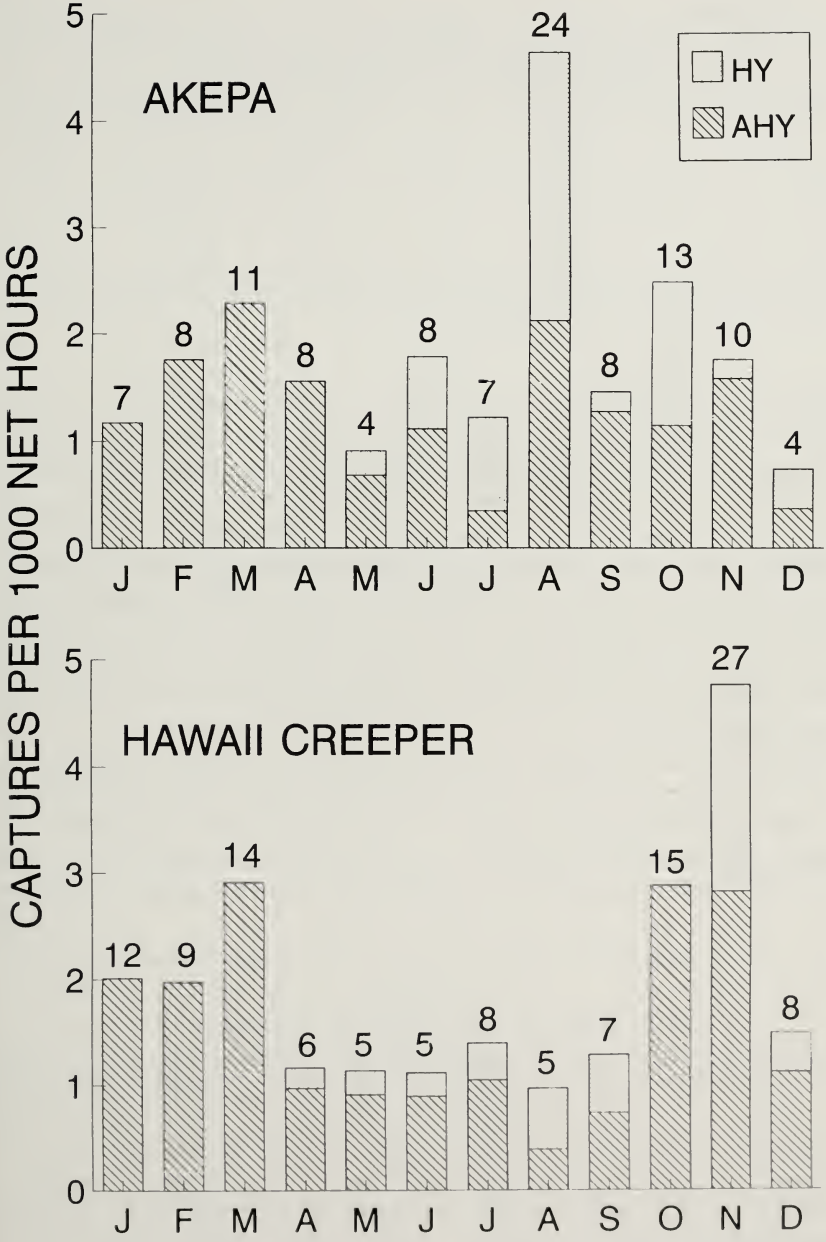

FIG. 5. Capture rates at Keauhou Ranch. Total number of birds captured each month is shown above each bar.

TABLE 2
NUMBER OF MONTHS INDIVIDUALS WERE OBSERVED

Species	Age at first capture[a]	N	Mean	SE	Range
Akepa	HY	30	6.8	1.82	1–40
	AHY	52	10.5	1.73	1–58
Hawaii Creeper	HY	20	10.9	3.43	1–53
	AHY	38	18.4	2.72	1–57

[a] HY = hatching year; AHY = after hatching year.

Forest study areas, where densities were at least three times as high as those at Keauhou Ranch and Kilauea Forest. Our density estimates for Akepa and Hawaii Creepers were higher than those obtained by Scott et al. (1986), partly because Scott et al. (1986) surveyed much larger areas and included transects where each species was absent or occurred in low numbers. Our study areas were intentionally located where these species were relatively common. Mueller-Dombois et al. (1981b) reported density estimates of 0.43 birds/ha for Akepa and 0.50 birds/ha for Hawaii Creepers at a site near our Kilauea Forest study area, but they used variable distance strip transects to estimate densities, and their results may not be directly comparable to ours.

Scott et al. (1986) found the highest density of Akepa (3.0 birds/ha) in subalpine ohia woodland in Kau during surveys in May and June 1976. We obtained a density estimate of 5.74 Akepa/ha in a nearby ohia forest at Kau during 1979–1980. Within the 1700–1900 m elevation band of their Hamakua study area, Scott et al. (1986) reported densities for Akepa and

TABLE 3
MOVEMENTS OF AKEPA AND HAWAII CREEPER

Sex	N	Home range size (km^2)		Median distance (m)[a]	
		Mean	SE	Mean	SE
Akepa					
Males	11	4.49	0.86	82.04	5.63
Females	7	3.07	0.47	75.18	4.78
Hawaii Creeper					
Males	10	7.93	1.38	104.63	6.24
Females	6	7.94	2.36	104.30	12.41

[a] Median distance from the center of activity to all locations.

Hawaii Creepers of 0.83 and 0.61 birds/ha, compared to our estimates of 1.35 and 1.79 birds/ha, respectively. Our study area is now part of the Hakalau Forest National Wildlife Refuge which was established primarily to protect some of the best remaining habitat for Akepa, Hawaii Creepers, and the Akiapolaau (*Hemignathus munroi*).

Sakai and Johanos (1983) suggested that Hawaii Creepers prefer relatively undisturbed koa-ohia forests, based on their finding of 1.62 nests/person·year of effort in our Kilauea Forest study area versus only 0.07 nests/person·year at the more disturbed Keauhou Ranch site. However, we found comparable densities of Hawaii Creepers at the two study areas, and capture rates of Hawaii Creepers at Keauhou Ranch were higher than those at Kilauea Forest (paired *t*-test, $t = 3.14$, $P = 0.009$). Furthermore, the density of Hawaii Creepers was similar at Hamakua and Kau Forest study areas, and yet Kau Forest has a largely intact native understory, whereas the Hamakua study area lacked a native understory because of intensive grazing.

Scott et al. (1986) reported a strong relationship between the presence of Hawaii Creepers and koa trees, and found that Hawaii Creepers in their Hamakua study area were nearly five times more common in koa-ohia than in ohia. Our Kilauea Forest site had more koa than the other three sites, and yet densities of Hawaii Creepers at Kilauea Forest were much lower than at Kau Forest or Hamakua. Thus, differences in density among sites cannot be explained only by the extent of disturbance to the understory or the availability of koa, and additional research is needed to understand why densities of Hawaii Creepers differ greatly among study areas.

Our estimates of annual survival (0.70 for Akepa and 0.73 for Hawaii Creepers) are similar to those reported by Freed (1988) for Akepa, Ralph and Fancy (1994b) for adult Omao (*Myadestes obscurus*), and Ralph and Fancy (unpubl. data) for Apapane (*Himatione sanguinea*). Freed (1988) calculated an adult survival rate of 0.77 for Akepa in the Kau Forest based on recaptures of three of five Akepa banded two years earlier. Annual survival rates of Akepa and Hawaii Creepers are near the upper end of the range of survival estimates reported by Karr et al. (1990), using the same methods of analysis, for 35 species of birds in temperate and tropical forests.

Our data on movements and activity of Akepa and Hawaii Creepers are consistent with the hypothesis that these species defend Type-B territories (Nice 1941) that are typical of cardueline finches (Newton 1972) and several species of Hawaiian honeycreepers. On Kauai, Eddinger (1970) found that Common Amakihi (*Hemignathus virens*), Anianiau (*H. parvus*), Apapane, and Iiwi (*Vestiaria coccinea*) all defended small areas around the nest during the breeding season but did not defend feeding territories. Male

Laysan Finches (*Telespiza cantans*; Morin 1992) and Palila (*Loxioides bailleui*; T. Pratt, unpubl. data) similarly defend mates and nest sites, but not food resources. Among Hawaiian honeycreepers, Type-A territories have been documented only for Common Amakihi (Baldwin 1953, van Riper 1987) and Akiapolaau (T. Pratt, unpubl. data).

Habitat loss and modification, introduction of avian diseases, predation by introduced mammals, and competition from alien species have all been cited as causes of the rapid decline of Hawaiian forest bird populations (Warner 1968, Atkinson 1977, Berger 1981, Mountainspring and Scott 1985, Ralph and van Riper 1985, Scott et al. 1986). In the recovery plan for the Akepa and Hawaii Creepers (USFWS 1982), the elimination and alteration of native forest ecosystems by feral ungulates and man were considered to be the most serious threats to these species. Studies of the effects of avian malaria and avian pox on native Hawaiian forest birds (Warner 1968; van Riper et al. 1986; C. Atkinson, unpubl. data) have confirmed that Hawaiian honeycreepers are highly susceptible to these diseases.

The remaining strongholds for Akepa and Hawaii Creepers appear to be higher-elevation native forests where mosquitos, the primary vector for avian malaria and pox, are absent (Scott et al. 1986; van Riper et al. 1986; C. Atkinson, unpubl. data; J. Lepson and L. Freed, unpubl. data). In suitable habitat, Akepa and Hawaii Creepers appear to be able to sustain relatively high densities with high adult survival. Although many aspects of the life history and demography of these two endangered species are poorly understood, the most obvious conservation strategy appears to be the protection of Hawaii's remaining native forests above the zone of mosquito occurrence.

ACKNOWLEDGMENTS

We thank the many field crew members who assisted with this study and, in particular, we thank Dawn Breese, Marc Collins, Peter Paton, Tim Ohashi, Howard Sakai, and Claire Wolfe for their efforts. We thank Tonnie Casey, Lenny Freed, Jeff Hatfield, Jaan Lepson, Thane Pratt, Mike Scott and Charles van Riper III for helpful comments on an earlier draft of the manuscript.

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BREEDING BIOLOGY AND HOME RANGE OF TWO *CICCABA* OWLS

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Abstract.—Thirteen Mottled Owl (*Ciccaba virgata*) nests are described from Tikal National Park, Peten, Guatemala. These were cavities in live trees at a mean height of 12.9 m. Mean clutch size was 2.2 (range 2–3). Nine nests fledged 16 young. Young left the nest at 27–33 days of age. Mean home range size was 20.8 ha (85% harmonic mean) for six radio-tagged breeding males, and density was seven breeding adults per km^2. Mottled Owls were found to be highly territorial, sedentary, and monogamous. Four nests of the Black-and-white Owl (*C. nigrolineata*) are also described. All were in epiphytes in large, live trees. Mean nest height was 20.5 m. Each nest contained one egg. The home range size of a single radio-tagged male was 437.3 ha (85% harmonic mean). One pair studied during three consecutive years was found to be monogamous and completely sedentary. *Received 14 Sept. 1993, accepted 11 Feb. 1994.*

Wood owls of the genus *Ciccaba* are poorly known, and data have been largely limited to morphological descriptions. Detailed information on natural history has been reported for only one species, the African Wood Owl (*C. woodfordii*), found only in Africa and the sole Old World representative of the genus (Steyn and Scott 1973; but see Amadon and Bull 1988, who place this species within *Strix*). New World *Ciccaba* inhabit Neotropical forests where they are mostly unstudied (Burton 1973).

The Mottled Owl (*C. virgata*) is believed to be the most numerous and widespread wood owl of the neotropics and subtropics; its range extends from Chihuahua and Sonora, Mexico, to northern Argentina and southern Brazil (Peterson and Chalif 1973). It has also been reported from Hidalgo County, Texas (Lasley et al. 1988). The literature contains few references to nests of the Mottled Owl (Belcher and Smooker 1936). Despite being widespread and numerous, virtually nothing is known of its breeding biology.

The Black-and-white Owl (*C. nigrolineata*) inhabits humid lowland and foothill forests from southern Mexico to northwestern Venezuela and northwestern Peru. It is uncommon to rare throughout its range (Peterson and Chalif 1973, Stiles and Skutch 1989). The literature mentioning this species is mostly brief anecdotal descriptions and individual accounts

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(Land 1963, Grossman and Hamlet 1964, Smithe 1966, Burton 1973). Much of the natural history of the Black-and-white Owl, including nests and breeding biology, has not been described.

We studied nesting Black-and-white Owls in Tikal National Park, Guatemala. Presented here are the first descriptions reported in the literature of the nests and eggs of this species and an estimate of home range size for a male based on radio-telemetry. We also describe nests, clutch size, and reproductive success of Mottled Owls in this same study area. We report home range size, present an estimate of breeding density, and discuss such characteristics of population dynamics as territoriality and monogamy.

STUDY AREA AND METHODS

We studied owls in Tikal National Park (576 km^2) in the Department of Peten in northeastern Guatemala (17°13′N, 89°38′W). Climate, physiography, and vegetation were described by Gerhardt et al. (1994). Owls were located by walking established trails within the park at dusk or dawn and listening for vocalizations. We found diurnal roosts by arriving at areas of previous activity at least 0.5 h before sunrise and listening as the owls called. Most Mottled Owl nests were found after hearing the female's food solicitation call, given from near the nest shortly after sunset. We found two nests after radio-tagging females. We located Black-and-white Owl nests by watching males leave their roosts at dusk. Prior to hunting, they typically flew to the nest tree and vocalized.

Once nests were located, we attempted to trap the adults using bal-chatri traps baited with mice or rats and placed either near the nest or under the bird's diurnal roost. We trapped female Mottled Owls by placing hoop-shaped mist nets over the nest cavity, and a male Black-and-white Owl was captured using a noose wire on a roost branch.

We affixed 3.5-g Holohil Systems Ltd. (Woodlawn, Ontario) transmitters to the central rectrices with thread and epoxy. Several Mottled Owls pulled the rectrices out, however, and we subsequently affixed transmitters as backpacks (Kenward 1987), using satin ribbon as the harness, sewed together with cotton thread.

We typically radio-tracked owls beginning the night after trapping. We followed each male owl and each non-nesting female for one hour every night and determined locations every 15 min. Radio-tracking was done on foot, using hand-held three-element yagi antennas and Falconer RB4 receivers. In most cases, a two-person team was able to observe and determine the location of the owl directly. Rarely was it necessary to triangulate to determine a location. All hours of the night were equally represented in 11-night regimes of random sampling. We followed owls sequentially in a given night, beginning with the bird farthest from the base camp. The hour of tracking this first bird was randomly chosen, and determined the schedule for following each of the other radio-tagged owls in the 11-night rotation. We followed as many as five owls in a given night, while only a single location was determined each night for nesting females.

We also located radio-tagged birds daily at their roosts. We used both diurnal and nocturnal locations in home range determinations. Owls were followed until their radios failed or were lost or until 15 Aug. (in 1989 and 1990) or 30 Aug. (in 1991).

We estimated home range areas using minimum convex polygon (Mohr 1947) and 85% harmonic mean (Dixon and Chapman 1980) methods generated by the computer program

HOMERANGE (Samuel et al. 1985). Owl density was determined by an extensive search for all pairs in the study area.

We climbed to Black-and-white Owl nests during the hour before dusk to minimize heat stress on nest contents. Mottled Owl nests were generally checked during late afternoon. We weighed eggs (to the nearest 0.5 g) with a 100-g Pesola scale and measured length and width (to 0.1 mm) with vernier calipers. Nest site characteristics—height, length, width, and depth of the cavities and tree height and diameter at breast height—were recorded after fledging had occurred. We report values throughout as means ± standard deviations.

RESULTS

Nests and eggs of Mottled Owls.—Thirteen active nests were located, seven in 1990 and six in 1991. Eggs were laid during March except in one nest in which eggs were laid in late April. The last fledgings occurring by the last week of May (the one later nest had failed by that time). While all seven pairs monitored in 1990 nested, only six of 11 did so in 1991.

All nests (N = 13) were in live trees. Most cavities (N = 10) were in the trunk itself and were formed by the rotting of a branch. One cavity was formed by the breaking of the trunk itself. This nest was open above, but was partly protected both by a branch of the nest tree that reached above and by the large leaves of a climbing vine (*Philodendron* sp.). Two other nests were in the main crotch of the tree. One of these was a depression only 10 cm deep, but it, too, was overhung by a *Philodendron.* Mean entrance size was 17.2 × 32.3 cm (N = 12; range = 8.0 × 16.0–30.0 × 40.0 cm) and the mean depth was 62.3 ± 61.3 cm (N = 13; range = 10–250 cm).

Nine species of trees were used as nests. *Pimenta dioica* and *Brosimum alicastrum* were used four and two times, respectively. Mean nest height was 12.9 ± 3.3 m (N = 13; range = 8.4–17.5 m) above ground.

Mean clutch size for 13 nests was 2.2 ± 0.14. All eggs were non-glossy, off-white, and elliptical, being only slightly longer (mean = 42.2 ± 2.2 mm) than wide (mean = 36.1 ± 0.7 mm; N = 16). Mean egg mass was 28.2 ± 1.8 g (N = 16).

Incubation apparently began with the laying of the first egg; females remained in the cavity beginning at that time, and young hatched asynchronously. Incubation period was not determined, but two eggs hatched after a minimum of 28 days. Females did all of the incubating and brooding, and males did all of the hunting. Even after brooding had ceased, females remained near the nest while males foraged.

Development of young Mottled Owls.—At hatching, nestlings had closed and protruding eyes and swollen (yolk-filled) abdomens. White natal down originating from the major feather tracts (pterylae) covered most of the nestling's body, whereas areas of bare skin (apteria) covered the remainder of the body. The cere and feet were flesh-colored and talons

were grey. The beak was grey with a small white egg tooth that disappeared by day six. About 8–10 days of age, young began to open their eyes and to tongue-click. At this time, the head and, more particularly, the orbital region, were the most thickly-feathered portions of the young owls (second generation down).

Prejuvenal molt began at 10–12 days of age. Contour feathers similar to those of adults appeared on the wings and back, and the tail began slowly growing in. The rest of the owl chick became covered in soft down and semiplumes, the body being of a peach or golden hue and the head creamy white. The first prebasic molt was not detected until four months of age, when adult-plumage contour feathers began appearing on the head and breast. This molt likely began earlier, but we did not capture fledglings to inspect them.

Three young fledged between 27 and 29 days after hatching and another at 32 or 33 days of age. Ten young weighed within three days of fledging had a mean body mass of 190.6 ± 19.9 g. Seven adult males and nine adult females had mean body masses of 239.7 ± 13.3 g (range = 220–256 g) and 335.6 ± 13.7 g (range = 308–366 g), respectively. Young were not observed on branches outside the nest prior to fledging. When fledging, the young owls were incapable of sustained flight, but merely glided downwards, either landing in low vines or underbrush or reaching the ground. They then climbed up into brush or leaning trees. These fledged owls never returned to the nest. Three months after fledging, young were still in the natal home range, roosting with and being fed by one or both of their parents.

Reproductive success of Mottled Owls.—Nine of the 13 nests (69%) fledged at least one young. Of the two 1990 nest failures, one female abandoned the nest during incubation, and the other nest was preyed upon when the chicks were two weeks old. In 1991, one nest was preyed upon by a mammal during incubation. Another nest was preyed upon one week after the hatching of the first chick. The second egg had disappeared just before it was due to hatch, and the adult female, captured at this time, had the quill of a porcupine (*Coendou mexicanus*) in her feathers. It is possible that this porcupine was involved in the partial and/or the eventual complete failure of this nest.

Home range, roosts, and territoriality of Mottled Owls.—Seven males and four females were radio-tagged. Two females pulled out their central rectrices and radios prior to nesting, and the two other females incubated and brooded for most of the life of their transmitters. We did not calculate home ranges for these nesting females.

Two of the seven males also molted their central tail feathers before sufficient data could be recorded. One was retrapped and equipped with

a backpack transmitter. Home range size was estimated for six males, four in 1990 and two in 1991. These were followed for 81, 63, 25, 61, 27, and 33 night-h and, with diurnal roost locations included, yielded 399, 301, 117, 294, 128, and 115 total locations, respectively. Mean home range size was (Fig. 2) 20.8 ha (85% harmonic mean) and 21.7 ha (minimum convex polygon).

Breeding density in the 2-km^2 1990 study area was 14 adults, or seven adults per km^2. In 1991, 11 pairs of adults were found in an area of 2.5 km^2. As has been reported, only six of these pairs actually attempted nests. The other five pairs, however, each engaged in copulation and territorial advertisement. If these are included, the 1991 estimate of density (territorial adults) was 8.8 adults per km^2. Of five pairs identified in the second year, only one female was a new owl.

Two hundred seventy-four different diurnal roosts were located on 407 occasions. The typical perch was a horizontal branch or vine in a dense section of wooded swamp. Mean diurnal roost height was 5.3 m (range = 0.5–18 m; N = 407). Cavities were never used for day-time roosting. Mottled Owls often spent the day within 2 m of the forest floor, particularly on the hottest day, and, when not on nests, females tended to roost with their mates, and later, family groups roosted together. Members of a pair or family were often found roosting within 1 m of one another. While females were on nests, males generally roosted a considerable distance away (mean = 252 m; N = 114), neither at the center nor at the perimeter of their home ranges.

We climbed to nests during late afternoon. Nest defense varied in intensity among females. Two females struck the climber repeatedly on every occasion. Another attacked the climber initially, but apparently became accustomed to the climbing and ceased striking. Four other females never struck but remained nearby, tongue-clicking and vocalizing. One female flew a considerable distance from the nest and roosted. One female sat tightly on the nest, and we were forced to pick her up to examine her eggs. Only on one occasion did a male arrive in apparent response to a female's vocalizing.

Nests and eggs of Black-and-white Owls.—Four occupied nests were found, one in 1989, two in 1990, and one in 1991. Three nests were in the same territory from 1989–1991 and attended by the same banded male (1989–1991) and same female (1990–1991). The female was captured in the 1990 season. The 1991 nest was 300 m from the 1989 nest and 450 m from the 1990 nest. All three nests were near the edge of an extensive bajo (wooded swamp). The second 1990 nest was in transition zone forest near a large bajo and approximately 3.5 km from the other three nests. The four nests were between 175 and 200 m above sea level. Nests were

in three species of trees, two in puctes (*Bucida bucerus*), one in mahogany (*Swietenia macrophylla*), and one in ramon (*Brosimum alicastrum*). Mean DBH was 87.3 ± 32.6 cm. Mean tree height was 26.3 ± 7.1 m (range = 21–30 m), and mean nest height was 20.5 ± 5.8 m (range = 16–26 m).

Eggs were laid on bare epiphytes; there was no nest construction by the owls. Two nests were formed by the orchid *Trigonidium egertonianum,* one by the orchid *Mormolyca ringens,* and one by a bromeliad of the genus *Tillandsia.* Each nest contained one egg. Eggs were off-white, non-glossy, and elliptical and were laid on the roots or foliage at the center of the epiphytes (Fig. 1). Mean egg mass was 33.8 ± 2.3 g (N = 4); mean length and width were 46.4 ± 1.1 mm and 38.4 ± 1.1 mm, respectively (N = 4).

Nests were apparently initiated in late March, as all hatching occurred in the last week of April. We were unable to collect reliable data on incubation, brooding, and food delivered to the nest because darkness and vegetation limited our viewing. The females' periodic vocalizations from the nest and activity of the radio-tagged male indicated the female likely performed all incubation. A female captured in 1990 had a small single brood patch; the male of the pair did not.

Reproductive success of Black-and-white Owls.—None of the four nests fledged young. The 1989 nest failed when the single young disappeared at approximately 24 days old. In 1990, the egg in this pair's nest failed to hatch, while in 1991, the same pair's chick disappeared within four days of hatching. The second nest found in 1990 failed when that young disappeared within a week after hatching.

Home range and roosts of Black-and-white Owls.—One male was radio-tagged and followed from 13 Apr. to 1 Aug. 1989 (118 locations of which 56 were diurnal roost locations) and from 12 May to 7 July 1990 (90 locations, 42 diurnal roosts). The home range size of this male using the 85% harmonic mean method was 437.3 ha. The area contained within the minimum convex polygon formed by these locations was 261.6 ha. A 50% harmonic mean estimate yielded an area of high utilization of 78.2 ha. This area included the nest site, several well-used diurnal roosts, and two foraging areas.

The home range size of this male was also estimated using only that subset of locations that was obtained following nest failure in both years. This subset included 123 locations, 62 of them diurnal roosts. These data yielded home range size estimates of 175.9 ha (85% harmonic mean) and 116.4 ha (minimum convex polygon) and a 50% harmonic mean area of 50.8 ha. In other words, this male utilized a much larger area while his mate was on a nest than following nest failure.

The radio-tagged male was located 98 times at 37 different diurnal

FIG. 1. Black-and-white Owl egg in nest in the orchid *Trigonidium egertonianum.*

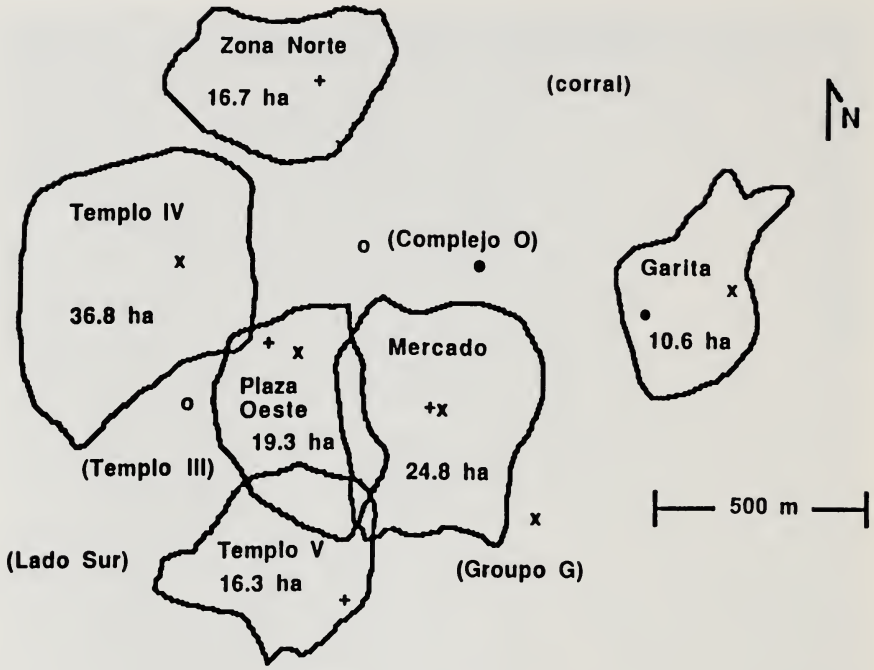

FIG. 2. Juxtaposition of home ranges (85% harmonic mean) and nests of Mottled Owls. x = successful nests in 1990; + = successful nests in 1991; ○ = failed nests in 1990; ● = failed nests in 1991.

roosts. Twenty roost trees were identified and included 10 species, of which zapotillo (*Diospirus* sp.), cedrillo (*Guarea* sp.), and ramon were most commonly used. Overhanging vines were a feature of many of these perches. Roost heights ranged from 3.5 to 26.0 m (mean = 14.0 m).

DISCUSSION

Ciccaba owls are reported to nest in tree cavities or in abandoned nests of other raptors (Burton 1973). Mottled Owls in this study used cavities for their nests. None of the Black-and-white Owl nests we located were in cavities or abandoned nests of other birds. In each case, the nest structure was a bare epiphyte, and we found no evidence to suggest that these sites had been used previously by other raptors. All Black-and-white Owl nests were in emergent trees, among the largest in the general vicinity. We believe neither snakes or mammals could reach these nests without climbing the nest tree itself. Indeed, the situation of all four nests seemed to make them more vulnerable to avian predators than to reptilian or

mammalian predators. Cavity nests of Mottled Owls were considerably lower than Black-and-white Owl nests and were not in lone or emergent trees. While such nests might still be vulnerable to avian predation, they are also more accessible to snakes and mammals.

Both Black-and-white Owls and Mottled Owls exhibited synchrony in their nesting, with nests being initiated and completed during the dry season. We have no data on the seasonal abundance or availability of their prey, and food supplies may certainly be a factor in nesting synchrony. It may be important that nesting be completed prior to the first hard rains because of the exposure of nests. Several Mottled Owl nests were situated such that rainwater collected where the eggs and young had been, and all Black-and-white Owl nests were exposed to the elements.

To date, no other owl species has been reported to have a clutch size of one, as did the Black-and-white Owls in this study. Clutch size tends to decrease with proximity to the equator, both within a species and between species of birds of similar taxa, size, and ecology (Moreau 1944, Lack 1966, Ricklefs 1969a). Our findings are in keeping with this tendency.

Of particular interest is the difference in home range size of these two sympatric congeners. This single Black-and-white Owl male had a home range more than 20 times larger than the mean home range size of the six male Mottled Owls. The difference in body size of these two species could account for at least some of this difference in home range size. We suggest, however, that the difference in food habits between these species plays a larger role in explaining this difference in home range. Both fed on large insects, particularly scarab beetles (Gerhardt et al. 1994). The vertebrate components of their diets, however, were quite different, with Mottled Owls eating small rodents and Black-and-white Owls capturing bats (Ibanez et al. 1992, Gerhardt et al. 1994).

It appears that Black-and-white Owls and Mottled Owls are monogamous and, as adults, sedentary. We suggest that Mottled Owls exhibit territorial defense of the entire home range, as has been reported for Barred Owls (*Strix varia*) (Nicholls and Fuller 1987). Overlap of home range among nonpaired birds amounted to no more than 20% of any pair's home range, while paired birds shared the same home range through two full seasons. Moreover, our observations of physical combat on the very edge of a radio-tagged male's home range supports the view that the entire home range is defended.

It is possible that the Black-and-white Owl is susceptible to human disturbance, and that the 100% failure rate was, at least in part, observer-induced. In general, however, tropical species are known to have a lower

fecundity and reproductive success than their counterparts in temperate zones (Ricklefs 1969b).

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DIET OF THE CHACO CHACHALACA

Sandra M. Caziani and Jorge J. Protomastro

Abstract.—Chaco Chachalacas (*Ortalis canicollis*) in the semi-arid Chaco forest region of northern Argentina fed mainly on herbaceous leaves (37% of the dry mass of its diet) and fleshy fruits (25%). Leaves and fruit were consumed year round. The rest of the diet consisted of caterpillars and flowers. The Chaco Chachalaca consumed all the fruit species available to it during this study period. Fruits most frequently eaten were: (1) fruit thickly bunched on the plant with long availability, even though of lower quality and (2) fruit of good quality (judged by pulp and total solids content). Low quality fruits not clumped together were less used in spite of their abundance in the forest. *Received 24 Feb. 1993, accepted 1 Mar. 1994.*

Guans (*Penelope*) and chachalacas (*Ortalis*) feed on leaves and fruit and probably are seed dispersers (Delacour and Amadon 1973, Terborgh 1986, Strahl and Grajal 1991). Marion (1976) found that fleshy fruit makes up approximately half of the diet of the Plain Chachalaca (*O. vetula*), a species also described as herbivorous-frugivorous by Christiansen (1978). Similarly, the Crested Guan (*P. purpurascens*) is one of the dispersers of wild nutmeg (*Virola surinamensis*), whose seeds it regurgitates (Howe and Vande Kerckhove 1980). In the forests of Northwest Argentina (El Rey National Park), the Dusky-legged Guan (*P. obscura*) feeds on various species of fleshy fruit in both summer and autumn (Brown 1986).

The Chaco Chachalaca (*O. canicollis*) inhabits the thorny Chaco forest of Bolivia, Paraguay, and Argentina where it is relatively abundant. There are no previous records of its feeding habits. In the woodlands of the western Argentine Chaco forest, the fruit supply is markedly seasonal and is most concentrated in the wet spring–summer season (Protomastro 1988). Winter is a time of shortage, both of water and of fruit and insects. The Chaco Chachalaca is the only fruit-dispersing bird living in the Chaco woodland throughout the year. Its diet is comprised mainly of plant leaves and fleshy fruits. Seeds pass through its digestive system intact and are probably viable at dispersion.

METHODS

We studied chachalacas in a second-growth woodland area of the 114,000 ha Copo Natural Preserve (25°55′S, 62°05′W), located in Santiago del Estero Province, Argentina. The vegetation is Chaco thorn forest (Cabrera 1976, Hueck 1978). Dominant tree species are quebracho colorado (*Schinopsis quebracho-colorado,* Anacardiaceae), quebracho blanco

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(*Aspidosperma quebracho-blanco,* Apocinaceae), and mistol (*Zizyphus mistol,* Rhamnaceae). The forest is interspersed with strips of natural grassland lying in ancient water courses. Ten of the 24 species of trees and bushes found in the area provide fleshy fruits or arillate seeds for the bird community (Protomastro 1988). Nevertheless these species do not bear fruit every year. There are marked seasonal changes in rainfall and temperature in the area. Eighty percent of the annual rainfall (650 mm) occurs in the wet season which lasts from October through March. Mean annual temperature, measured at the nearest weather station (Campo Gallo, 120 km to the SW), was 21.9°C, and the average maximum and minimum temperatures determined for January (summer) and July (winter) were 35.5°C–20.2°C and 23.0°C–7.1°C, respectively (1951–1980, Servicio Meteorológico Nacional of Argentina).

Between March 1986 and April 1987, a total of 29 Chaco Chachalacas were collected (1–4 per month), one of them a young. We collected them in a secondary forest area of approximately 20 ha. There were ecotones with natural grassland near the area. A greater number of specimens was not taken because sampling was carried out in a wildlife reserve. We weighed and measured the birds and identified sex and reproductive state. Esophagi, gizzards, and intestines were preserved in 70% ethyl alcohol. In the laboratory we separated and identified the items, which were oven-dried at 40°C and weighed (±0.1 mg). We identified and counted seeds found in digestive tracts and recorded their condition in order to estimate potential dispersal. Potentially dispersable species were considered to be those which we observed in the intestine without visible damage.

The abundance of woody plants with fleshy fruits and arillated seeds was quantified along a transect 1000 m long by 4 m wide. Once a month, we counted the number of plants with ripe fruits, green fruits, or without fruits. The number of individuals analyzed according to their abundance in the forest varied from 10 to 143.

The total fresh mass, fresh seed mass, and net pulp mass (by subtraction) of the ripe fruit were determined, as was the major cross-width (using calipers). The total solids percentage was obtained using a field refractometer. We used this measure as a quick approximation of nutrient reward of the pulp. Our field observations suggest that sugars are the principal reward. However, when refractometer readings are not specific for sugars, then we express the results as total percent of solids (White and Stile 1985). The fruit and seeds were group weighed on a scale (0 to 10 g); therefore, individual variation in mass could not be determined.

RESULTS

The average mass of adult specimens was 539 g, (±60 g, SD; N = 24). The dry mass of the esophagus and gizzard contents varied between 0.45 g and 9.70 g. Only seven individuals had food in the esophagus. The gizzard contents alone had an average mass of 2.62 g (±1.34 g, N = 29). Food items found in greatest proportions in the diet were herbaceous leaves and fleshy fruits, followed by caterpillars and flowers (Table 1). Herbaceous leaves and fruit made up 62% of the total dry mass of the diet of the Chaco Chachalaca, and they were consumed year round (Fig. 1). The proportion of fruits in their diet was significantly higher during the October through March wet season (Mann-Whitney one-tail test, $P < 0.01$). The proportion of leaves consumed showed no significant difference between dry and wet seasons. Caterpillars and flowers were consumed only during certain periods and the former consisted exclu-

TABLE 1
GENERAL COMPOSITION OF THE CHACO CHACHALACA DIET IN THE COPO PRESERVE, ARGENTINA

Food item	Dry mass as percentage[a]	Presence in esophagus-gizzard contents
Herb leaves	36.6	21/29
Vegetable remains	1.9	12/29
Total vegetable items	38.5	25/29
Molle fruit	12.1	12/29
Mistol fruit	4.0	3/29
Sangre de toro fruit	2.4	11/29
Tala blanca fruit	1.9	4/29
Tala fruit	2.2	7/29
Coro fruit	2.3	3/29
Total fruit items	24.9	25/29
Mistol caterpillars	22.1	6/29
Total animal items	22.1	6/29
Garabato flowers	3.7	3/29
Creeper flowers	1.5	5/29
Sacha naranjo flowers	0.3	1/29
Soft seeds	1.1	4/29
Total flowers and seeds	6.6	13/29
Stones	7.9	13/29
Total stones	7.9	

[a] Item dry mass/total dry mass of 29 samples × 100.

sively of one unknown butterfly, a caterpillar on mistol (*Zizyphus mistol*). This caterpillar abounds only in certain years, one of which happened to be that in which our sampling was carried out. Flower buds and flowers (particularly garabato [*Acacia* sp.] and Sacha Naranjo [*Capparis retusa*]) were found in the specimens sampled from June through December. Consumption coincided partly with peak availability of buds (late August and September) and flowers (September and October) (Protomastro 1988).

Chaco Chachalacas consumed the fruit of six plant species, five woody and one herbaceous (Table 2). The other five woody species did not bear fruit during the study year. Chachalacas used fleshy fruits whenever they were available. The fruits were eaten when ripe, with the exception of green tala drupes (*Celtis pallida*), eaten at the end of October 1986, and some green molle (*Schinus polygamus*) drupes mixed with the ripe fruit. Small seeds were defecated, and the large ones were probably regurgitated

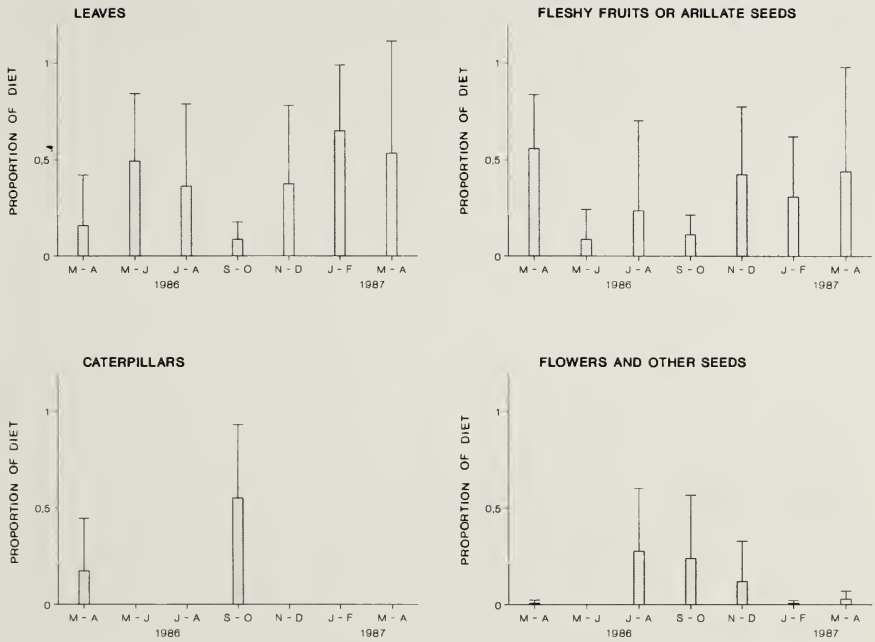

FIG. 1. Proportions of main food item types in esophagus and gizzard contents in bimonthly periods. Average proportion and standard deviation are shown. The number of Chaco Chachalaca for each period were: M–A = 6, M–J = 5, J–A = 4, S–O = 5, N–D = 4; J–F = 3, M–A = 2.

TABLE 2

PLANT SPECIES CHARACTERISTICS

Species	Habit (height)	Number of fruits per plant	Basal area in forest[a]
Molle	Bush (6 m)	5000 to 100,000	0.3
Tala	Bush (2 m)	10 to 300	1.3
Tala blanca	Bush (3 m)	1000 to 50,000	2.1
Mistol	Tree (6 m)	50 to 500	6.5
Coro	Tree (4 m)	20 to 500	0.2
Sangre de toro	Herb (50 cm)	50 to 250	no data

[a] Stem and trunk basal area in m^2 per ha, mean of 7 plots of 225 m^2 (Protomastro 1988).

(mistol and coro [*Jodina rhombifolia*]), because they were never found in the intestine.

Molle was the most commonly consumed fruit and appeared in 12 birds in spite of its low basal area in the forest (Table 2), few fruiting plants (Fig. 2) and low pulp mass (Table 3). However, molle has thousands of fruits on each plant and has long fruiting periods of three months. Mistol fruit contained the greatest net pulp mass and the highest total percent of solids (Table 3). We did not find any mistol tree bearing fruit in our sampling despite its high basal area. In another sampling (Protomastro 1988), only one of ten specimens bore scarce ripe fruit in the same area and time. However, some individuals located at the forest-grassland edges (near the study area) carried large quantities of fruit. The other four species were eaten in similar proportions. The tala had a large number of fruit-bearing individuals (Fig. 2), which agrees with its large basal area in the forest (Table 2), but it bears only a few drupes per plant. Two peaks of fruit availability (Fig. 2) fell within a single variable fruiting period lasting from December to March. Tala blancas (*Achatocarpus praecox*) have thickly bunched fruits with many drupes per plant. Fruiting periods of tala blanca and coro trees are November–December and September–October, respectively (Fig. 2). Sangre de toro (*Rivina humilis*) fruit was used mainly in the May–June period but appeared in stomach contents in November, December, February, and April as well. It was the only available fruit in the May–June period. We did not measure the bi-monthly number of fruiting herbs but sangre de toro fruiting period seems to be very broad.

Fruits of molle and tala blanca shrubs were found in great quantities in gut contents (median 117.5 fruit [12 samples] and 47.5 fruit [4 samples], respectively). This agrees with the high frequency of the fruits on these plants. Sixteen digestive tracts contained one fruit species, and only four contents had three to four fruit species. In six of twelve samples with molle this fruit appeared with fruits of mistol, tala, sangre de toro, or tala blanca.

We observed that Chaco Chachalaca fed in groups. The birds remained on shrubs or trees and walked on the ground in open sites or tracks. In the evening, they slept in trees. Chaco Chachalacas breed during the rainy season. Egg laying probably occurs during December, as one mid-December specimen contained a half-formed egg, 20 mm in diameter. In addition to 28 adults, collected at the beginning of January, a chick weighing 150 g was collected accidentally and a young chachalaca weighing 270 g was obtained at the end of February. In February, many groups with young were observed on the roads. During the period considered to be that in which the chicks were being fed (December–January), no food of animal

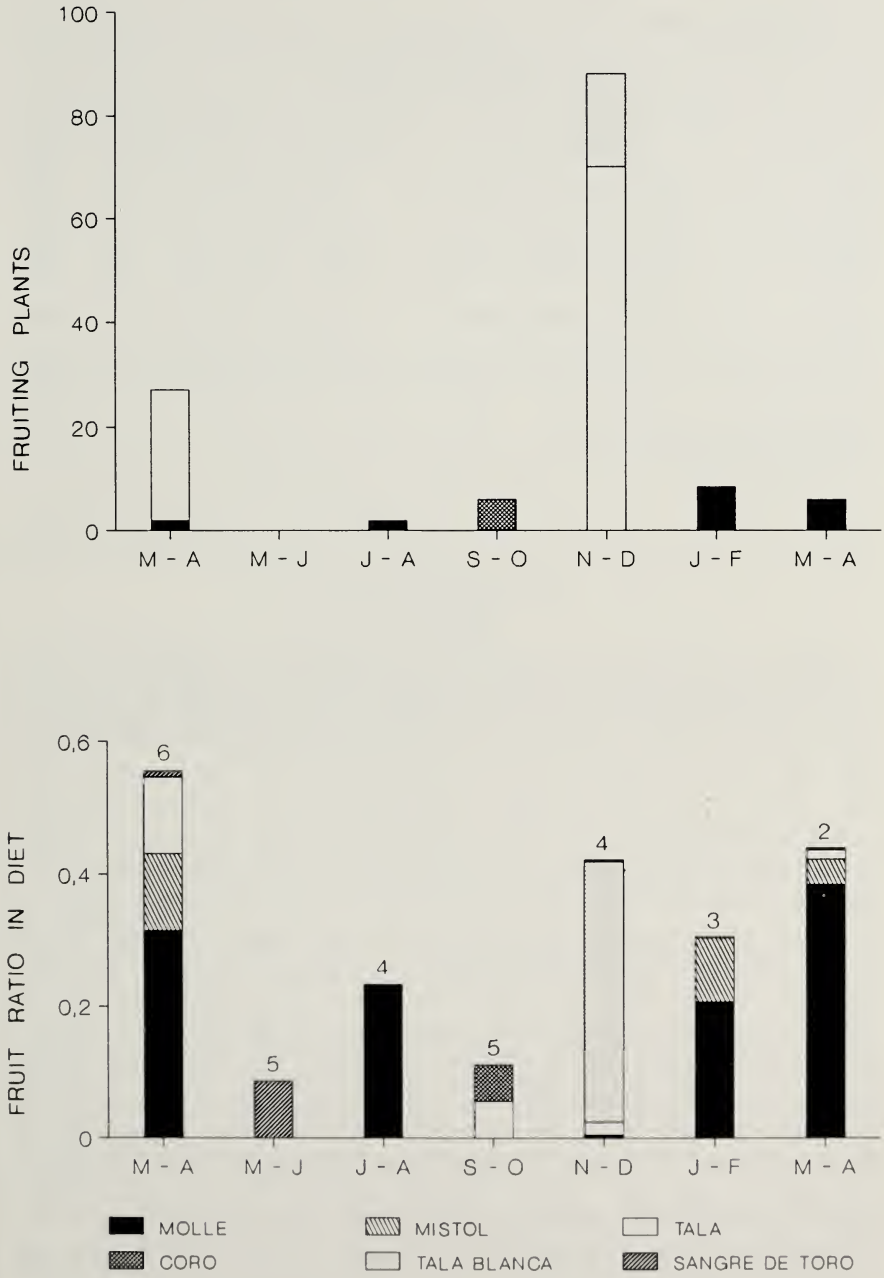

FIG. 2. Proportional fruit availability and fruit consumption by the Chaco Chachalaca. Availability is shown as the bi-monthly average of fruit-bearing individuals along the phenology track. Consumption is shown as the average (bi-monthly) proportion of the dry weight of different fruit species.

TABLE 3
FRUIT CHARACTERISTICS

Species	Type and color of fruit	Diameter in mm[a]	Fresh mass[b]	Pulp in g[c]	Total solids[d]
Molle	Purple drupe, one seed	4.3 ± 0.1	0.03	0.02	20%
Tala	Orange drupe, one seed	7.3 ± 0.3	0.19	0.16	17%
Tala blanca	Translucent drupe, one seed	6.8 ± 0.2	0.18	0.17	21%
Mistol	Red drupe, floury pulp, one seed	10.8 ± 0.3	0.77	0.66	40%
Coro	Red capsule, one seed[e]	7.1 ± 0.3	0.28	0.17	15%
Sangre de toro	Red berry, 1 to 3 seeds	Approx. 5	—	—	—

[a] N = 20.
[b] In g.
[c] Total fresh weight, less fresh mass of seed.
[d] Measured with field refractometer.
[e] Diameter of seed with aril.

origin was observed in gizzard contents (N = 3). The chick contained 1.2 g of food including leaves, tala blanca, and flowers.

DISCUSSION

Leaves were a very important resource (37% of dry mass). We found no woody plant leaves, which have high levels of secondary compounds (Protomastro 1988); all leaves were eaten by chachalacas from herbaceous plants. In the wet season, such leaves are common, but in dry season they grow only in humid microhabitats which are scarce. The Chaco Chachalaca used good quality fruit (with highest pulp and total solids percentages) or that which was abundantly bunched. This seems logical for large-sized birds which obtain their food by perching in trees and bushes and feeding in groups, taking into account the cost of travel, maneuvering, and access in fruit selection (Moermond and Denslow 1983, Levey et al. 1984, Martin 1985). In the field, we noticed that the Chaco Chachalaca re-visits plants or groups of plants bearing abundant fruit. Moreover, the majority of gut contents (60%) had only one fruit species. This was most frequent in the case of the most commonly eaten fruit, molle. The fruit of this plant grows in profusion on each plant, and the plants are grouped in low-lying areas having a greater moisture content in the soil (Protomastro and Caziani, pers. obs.). The fruiting period of molle is very prolonged, which favors extensive foraging of the same group of bushes.

During the winter, molle fruit seems to be a key resource like herb leaves and sangre de toro fruit. Chaco Chachalacas were the only dispersers of the coro fruit and of the molle plants fruiting in the dry season. Seeds were found intact throughout the digestive tract. The summer-fruit-

ing molle, the tala, and the tala blanca have other avian dispersers, in addition to the Chaco Chachalaca, including the Creamy-bellied Thrush (*Turdus amaurochalinus*), Small-billed Elaenia (*Elaenia parvirostris*) and White-crested Elaenia (*E. albiceps*). These birds are summer visitors that arrive in the forest in September and remain there during the wet season; their visits thus coincide with the period in which fruit is most abundant (Caziani 1987 and unpubl. data). The mistol tree has other dispersers, such as the red iguana (*Tupinambis rufescens*) and the southern three-banded armadillo (*Tolypeustes matacos*) (Bolkovic et al. 1989). We suspect that Chaco Chachalacas are more abundant in secondary woodlands (selective logging), because we heard many groups of birds singing in the morning (more rarely in the evening) in this kind of forest but not in pristine woodlands. Characteristics which could explain this pattern are (1) the Chaco Chachalaca seems to prefer open places which are common in exploited woodland and (2) fruit density of tala blanca and tala is significantly greater in secondary forest (Protomastro 1988; Caziani and Protomastro, unpubl. data).

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GRADUATE AND POST-GRADUATE RESEARCH GRANTS

The Biological Research Station of the Edmund Niles Huyck Preserve offers grants (max. = $2,500) to support biological research which utilizes the resources of the Preserve. Among the research areas supported are basic and applied ecology, animal behavior, systematics, evolution, and conservation. The 2000 acre Preserve is located on the Helderberg Plateau, 30 miles southwest of Albany. Habitats include northeast hardwood-hemlock forests, conifer plantations, old fields, permanent and intermittent streams, 10 and 100 acre lakes and several waterfalls. Facilities include a wet and dry lab, library, and houses/cabins for researchers. Deadline = February 1, 1995. Application material may be obtained from Dr. Richard L. Wyman, Executive Director, E.N. Huyck Preserve and Biological Research Station, P.O. Box 189, Rensselaerville, New York 12147.

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SEASONAL DISTRIBUTION AND NATURAL HISTORY OF THE PATAGONIAN TYRANT (*COLORHAMPHUS PARVIROSTRIS*)

R. Terry Chesser and Manuel Marín A.

Abstract.—We studied the distribution and ecology of the Patagonian Tyrant (*Colorhamphus parvirostris*), a migratory insectivorous passerine, using data from museum specimens, literature references, and personal observations. Our analyses indicated that *C. parvirostris* is associated primarily with southern beech (*Nothofagus* spp.) forest, and breeds along the western and eastern slopes of the Andes from Tierra del Fuego north to the Coronel/Pichinahuel area of Chile. The species winters mainly in central Chile, as far north as El Palomo and Ovalle, but small numbers winter between Concepción and Chiloé, within the species' breeding range. In winter, *C. parvirostris* occupies *Nothofagus* forest in the southern part of its range, but is found in riparian forest and woodland in central Chile. Several controversial nesting records for the species are considered and accepted, but the assertion that *C. parvirostris* occurs in eastern Argentina is shown to be in error. *Received 25 Oct. 1993, accepted 5 May 1994.*

Resumen.—La distribución y ecología del pequeño tiránido migratorio la Viudita (*Colorhamphus parvirostris*) fueron estudiadas usando información obtenida de especimenes de museo, literatura y observaciones personales. Nuestro análisis indica que la distribución de *C. parvirostris* está asociada primariamente con la distribución del bosque de *Nothofagus* spp. La especie nidifica en ambos lados de la Cordillera andina, desde Tierra del Fuego hasta la zona de Coronel/Pichinahuel en Chile. La gran mayoria de indivíduos pasan el invierno en Chile central, llegando como limite norte hasta El Palomo y Ovalle, pero algunos indivíduos permanecen durante el invierno entre Concepción y Chiloé, que está dentro de su área de nidificación. Durante el invierno *C. parvirostris* ocupa el bosque de *Nothofagus* en la parte sur de su distribución, pero en Chile central se encuentra en bosques y arboladas en quebradas húmedas. Varios registros de nidificación para la especie que han sido considerados polémicos, fueron revisados y aceptados. Se demuestra que la aseveración que *C. parvirostris* occurre al este de Argentina es un error.

The Patagonian Tyrant (*Colorhamphus parvirostris*) is a small, uncommon migratory passerine of Chile and Argentina, one of some 230 austral migrants, species that breed in southern South America and migrate north for the austral winter (Chesser 1994). The sole member of its genus, it was described originally by Darwin (1839) as *Myiobius parvirostris* and has been placed in the genera *Tyrannula* (Hartlaub 1853), *Serpophaga* (Sclater 1867), *Elainea* (*Elaenia* [as *E. murina*]) (Philippi 1895), and *Muscicapa* (Philippi 1902), in addition to *Colorhamphus* (Sundevall 1872 *in* Cory and Hellmayr 1927). More recently, Traylor (1977) merged the genus into *Ochthoeca*, as had Berlepsch (1907). Lanyon (1986) resur-

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rected *Colorhamphus* as the sister genus to *Ochthoeca* in his study of syrinx morphology in the *Empidonax* assemblage of tyrant-flycatchers, a view that was followed by Sibley and Monroe (1990). Although known to inhabit the eastern and western slopes of the southern Andes, the distribution of *C. parvirostris,* both breeding and winter, has been the subject of some controversy. Pässler (1922), for instance, reported two nests of this species near Coronel (Prov. Concepción, central Chile), but according to Hellmayr (1932) it is "extremely unlikely that the bird found breeding by Pässler . . . pertained to the present species" (p. 145). Likewise, Olrog (1963) indicated Buenos Aires (Argentina) in the breeding range of *C. parvirostris,* and Meyer de Schauensee (1966, 1970) and Sibley and Monroe (1990) reported the winter range as extending north to Buenos Aires. However, Traylor (1979), Narosky and Yzurieta (1987), and Fjeldså and Krabbe (1990) restricted the Argentine distribution of the species to the southwestern portion of the country.

Detailed analyses of distributional records have revealed that actual breeding and wintering ranges of migratory South American species can differ considerably from published accounts (e.g., Remsen and Parker 1990, Marantz and Remsen 1991). Here we analyze the seasonal and geographic distribution of *C. parvirostris* in detail, review all nesting records of the species, summarize its ecology, and present new distributional and ecological data.

METHODS

We obtained distributional data from museum specimens of *C. parvirostris,* from literature references, and from personal observations. We gathered data on specimens from South and North American museums housing major collections of Argentine and Chilean birds, and solicited data from museums that we were unable to visit personally (e.g., several European collections). Data taken from each specimen included locality, date, sex, collector, and any supplemental information. Geographical coordinates for localities were determined from the Argentine and Chilean gazetteers of Paynter (1985, 1988), and elevations, where not noted on specimen labels, were taken from the same sources. Chilean localities not in Paynter (1988) were obtained from maps. Localities cited in the text are followed by geographical coordinates (degrees and minutes south, degrees and minutes west) as in Paynter (1985, 1988). Chilean provinces are cited in accordance with the new "region and province system" of Chile. MMA gathered field data in Chile during January 1976 (austral summer) at Nahuelbuta and Pichinahuel (both Prov. Malleco), from January through March 1981 (austral summer) on Isla Chiloé (Prov. Chiloé), from April through September 1980 and May through September 1981 at El Portezuelo, Lo Barnechea, and Colina (Prov. Santiago), and Huilmo (Prov. Limarí), and during August 1993 (austral winter) at San Manuel (Prov. Melipilla).

RESULTS

Breeding distribution.—We located 123 specimens of *C. parvirostris* containing at least the date and locality of collection (Appendix I), and

TABLE 1

PUBLISHED RECORDS OF NESTS OF *COLORHAMPHUS PARVIROSTRIS*

Locality	Latitude (S)	Longitude (W)	Date	Contents	Source
ARG: Río Negro, Isla Victoria [ca 800 m]	40°56′	71°33′	26 Oct. 1984	In construction	Saibene 1988
			19 Nov. 1984	One egg	
ARG: Río Negro, Lago Hess [ca 800 m]	41°22′	71°43′	Jan. 1938	Three eggs	Zotta 1939
ARG: Río Negro, S.C. de Bariloche [767 m]	41°09′	71°18′	5 Jan. 1988	Three eggs	Casas 1990
			10 Jan. 1988	Two eggs, one nestling	
ARG: Chubut, Esquel [ca 1000 m]	42°54′	71°19′	15 Jan. 1987	One egg	Casas 1990
CHL: Tierra del Fuego, Tierra del Fuego	ca 54°00′	ca 69°00′	Dec. 1938	Two eggs	Johnson 1967
CHL: Concepción, Coronel [10 m]	37°01′	73°08′	22 Dec. 1915	Three eggs	Pässler 1922
CHL: Concepción, Coronel [10 m]	37°01′	73°08′	19 Jan. 1908	Two eggs	Pässler 1922
CHL: Malleco, Pichinahuel [ca 1200 m]	ca 37°40′	ca 73°00′	19 Jan. 1976	Three nestlings	Marín et al. 1989
CHL: Malleco, Pichinahuel [ca 1200 m]	ca 37°40′	ca 73°00′	19/20 Jan. 1976	Two nestlings	Marín et al. 1989
CHL: Malleco, Pichinahuel [ca 1200 m]	ca 37°40′	ca 73°00′	20 Jan. 1976	Two nestlings	Marín et al. 1989

10 purported nesting records (Table 1). Hellmayr (1932) additionally mentioned Isla Hoste and "along the Straits of Magellan" as nesting localities, but, although these localities are consistent with the specimen record, he provided no details for them. The record for the Straits of Magellan is apparently based on Stone's (1928) report of the collection of juvenile birds at Punta Arenas in January 1899 (see also Appendix I). Nesting records extend by date from 26 October, when the nest found by Saibene (1988) was under construction, to 19–20 January when three nests with nestlings were discovered (Marín et al. 1989). Of the specimen records, only six are from late October to January, with an additional four from February, when the species is still on its breeding grounds (see below), and eight from the breeding area in March. Almost all austral summer specimen records fall within the geographical extremes of the breeding records. Nest records indicate that the breeding range extends from southern Chilean Tierra del Fuego northward through southern Chile to the Coronel/Pichinahuel area (Regions VIII through XII) and east of the Andes in southwestern Argentina in the provinces of Chubut, Río Negro, and Neuquén. We also include the provinces of Santa Cruz and Tierra del Fuego, Argentina, in the breeding range on the basis of specimen records (Fig. 1). Breeding elevations extend from sea level to 1800 m (Hellmayr 1932).

Colorhamphus parvirostris appears to be uncommon throughout its breeding range. Olrog (1948) encountered it rarely in Tierra del Fuego and Province Magallanes. Philippi et al. (1954) failed to see or hear the species in Tierra del Fuego and heard it in Magallanes only twice, at Río Rubens (5154/7135) and Estancia Río Paine (5111/7258). Although he expected *C. parvirostris* to be present, Philippi (1939) did not find it in his travels in Aysén, nor did Riveros (1979) encounter it at Parque Nacional "Laguna San Rafael," Aysén. Clark et al. (1984) reported *C. parvirostris* to be scarce on Isla Guafo (4336/7443), and Barría (1972) described it as fairly scarce at two localities on Isla Chiloé between Dalcahue (4223/7340) and Mocopulli (4221/7343). During a survey of Isla Chiloé from January to March 1981, MMA found it uncommon and present only on the eastern side of the island. The species was also uncommon at Pichinahuel in January 1976. In Argentina, Saibene (1988) recorded it as scarce on Isla Victoria (4056/7133), where Contreras (1975) netted five individuals in February and March 1972 or 1973. Reynolds (1934, 1935) did not mention the species in his papers on the birds of Isla Grande. Although Humphrey et al. (1970) reported it "from but a few records," they cited only one specimen at one locality (Lapataia). Sielfeld (1977) found it extremely rare at the extreme southern limit of *Nothofagus* forest on Isla Hoste (5505/6850), and collected only one spec-

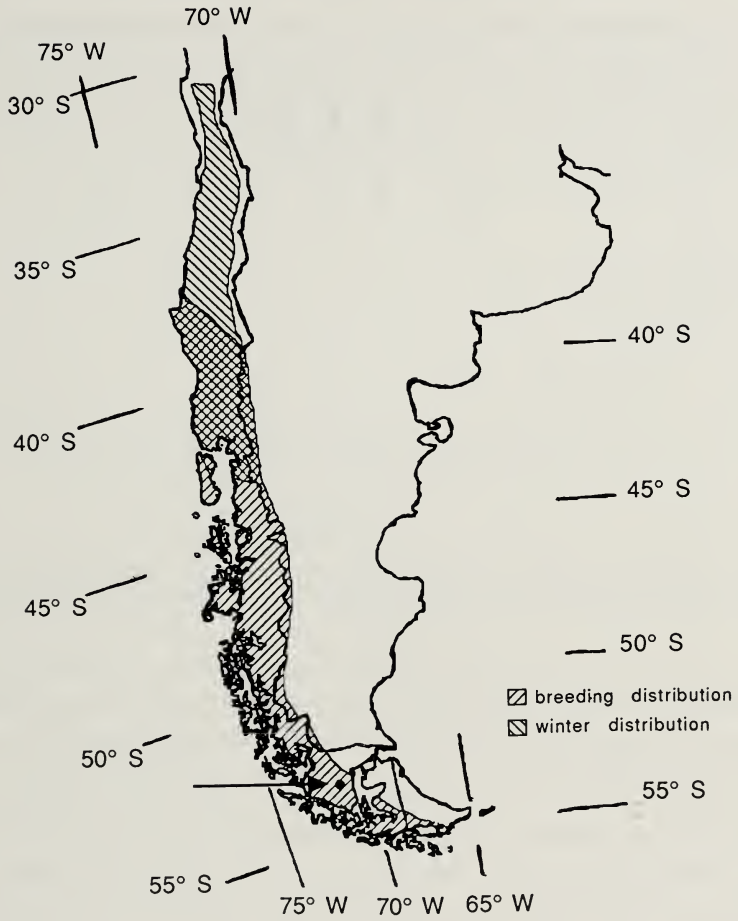

FIG. 1. Distribution of *Colorhamphus parvirostris*. The arrow and dot represent the winter specimen taken in June 1914 at Punta Arenas, more than 1000 km south of the next southernmost winter record.

imen. Likewise, Chebez and Gómez (1988) encountered it only once on Argentine Tierra del Fuego during December 1985 and January 1986.

Migration and winter distribution.—In winter, many individuals move north to occupy areas outside the breeding range, whereas small numbers remain within the breeding range (Figs. 1, 2). Such migration, characterized by partially overlapping breeding and wintering ranges, is typical of austral migrants (Chesser 1994). *C. parvirostris* extends its range northward in winter from the Concepción area in central Chile to Ovalle and El Palomo in the north (Fig. 1). The earliest records from the wintering

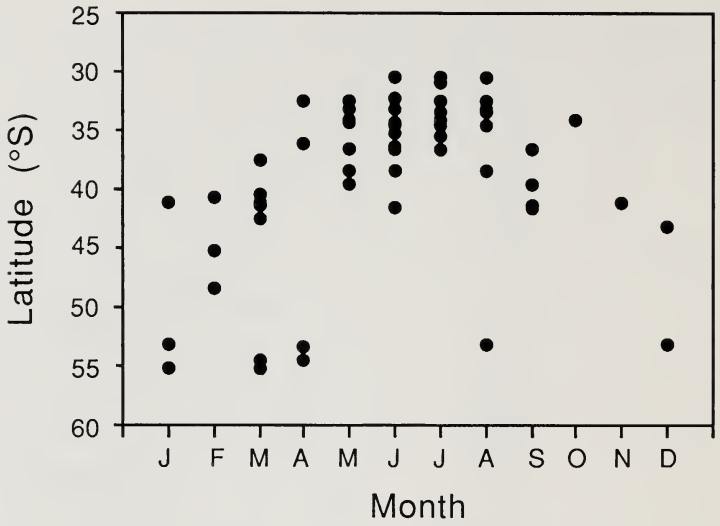

FIG. 2. Specimen records of *Colorhamphus parvirostris* by month of collection and latitude. Note especially the seasonality of occurrence at the northern end of its range.

range have been from late March; Barros (1966) reported individuals from Linares (3551/7136) on 21 March 1949 and 28 March 1948, and from the end of March in Río Blanco (3255/7019) and other parts of the Cordillera Aconcagua. In most years and most places, the first migrants reach the northern part of the wintering range in April (Barros 1920, 1921, 1966) after the first rains (Barros 1920), and by May the species is common (Barros 1921, 1966). Vuilleumier (in litt.) observed a single individual on 3 April 1965 in stunted Nothofagus forest at Termas de Chillan (3654/7131). At Colina (3312/7041) in 1981, the species first appeared on 27 April. Egli (1986) reported the first individuals at Rinconada de Maipú (ca 3331/7046) in April (1983, 1984) and May (1982). Except for the winter record from Punta Arenas (see below), late dates from the southern part of the breeding range are two specimens from Prov. Magallanes, Chile, on 17 April 1971 and one from Argentine Tierra del Fuego on 24 April 1971.

Winter records for *C. parvirostris* extend from Ancud, Chile (4152/7350), and El Bolsón, Argentina (4158/7131), in the south to Prov. Limarí, Chile, in the north, with the exception of a single specimen from Punta Arenas (5309/7055) in August 1914. Numerous specimens were secured at Huilmo (3050/7105) in 1981 and El Palomo (ca 3046/7110) in 1984, a northern range extension, the previous northernmost record having been from the Río Cenicero, Prov. Choapa (3128/7046) (cited by

Philippi [1964], but without date of collection). MMA also observed the species on the outskirts of Ovalle (3036/7112) in 1981, although no specimens were collected at this locality. Barros (1966) found *C. parvirostris* much more common in winter in mountainous areas than along the coast and saw it frequently in foothills and valleys to 2000 m and above. North of the Santiago region, the species is not found along the coast, where the habitat becomes xerophytic and scrubby.

The species is apparently rare during winter within the central and southern portions of its breeding range. Only one of the nine Argentine specimens is from winter—28 June 1961 from El Bolsón, Río Negro (4158/7131)—and Saibene (1988), who reported the species nesting in Río Negro province, did not observe it there during winter. A Chilean winter specimen from well within the breeding range was collected at Ancud (4152/7350), and Barros (1948, 1966) noted several birds during winter at Maullín (4138/7337) in 1948. The southernmost winter specimen, by more than 1000 km, was collected 3 Aug. 1914 at Punta Arenas (Fig. 1). Darwin (1839) reported collecting an individual of this species in June in Tierra del Fuego and indicated that it probably remains throughout the year in southern South America, but the bird is not in the British Museum (Sclater 1888; data from British Museum) with his other specimens and may have been misidentified.

Migration southward to the breeding grounds begins in August and continues through September (Barros 1920, 1966). Late dates for *C. parvirostris* on its wintering grounds include 11 Sept. 1949 in Linares (3551/7136), 8 Sept. 1937 at Conchalí (3153/7129), 4 Sept. 1953 along the coast of Province San Antonio (ca 33337/7137) (Barros 1966), and 6 Sept. 1981 at Lo Barnechea (3321/7031). An extremely late wintering bird was collected in Valle La Engorda (ca 3410/6950) on 12 Oct. 1961. The late date and high elevation (2700 m) of the specimen suggest that the bird was probably a vagrant. Olrog (1948) collected specimens during migration at Enco (3953/7211), 27 Sept. 1940, and migration continues into October, when individuals have been noted arriving at Isla Grande (Fjeldså and Krabbe 1990).

Natural history.—The nest and eggs of *C. parvirostris* were first described by Pässler (1922), and his paper contains the essential features of the nest as described by most observers. The first nest was cup-shaped, located 2.5 m above ground in a "Boldobusch" (*Peumus boldus*) and constructed of dry grass stems and plant fibers. The second nest was similar, but the exterior was lined with moss. Descriptions of nests by other authors (Table 1) approximate Pässler's description; nests are usually cup-shaped and situated low in a shrub, made of plant fibers, and lined outside with moss. Marín et al. (1989), for instance, described three

nests "in the thick understory of a beech (*Nothofagus*) forest, at 50–110 cm above the ground in 80–120 cm tall shrubs growing along creeks. They were cup-shaped structures of grass and moss, lined with fine grasses and some feathers." Pässler (1922) described the eggs as oval, white or light cream colored, with small, rusty red or reddish-brown spotting on the larger end, sometimes forming an irregular wreath. Dimensions of five eggs (Pässler 1922) averaged 19.2 × 15.1 mm (±0.6 × 0.3). These are again typical of the species.

The breeding range of the species coincides with the presence of *Nothofagus* forest as discussed in Vuilleumier (1985, 1991). According to Fjeldså and Krabbe (1990), the species breeds only in *Nothofagus* forest, and Vuilleumier (1985) listed it as endemic to Patagonian forests, ranging from rain forest and montane forest to mesophytic forest and parkland. Darwin (1839) found *C. parvirostris* in the forests of Tierra del Fuego, and Venegas and Jory (1979) noted that in Magallanes it is seen and heard only in areas of forest and woodland. During this season, at the extreme southern end of its range, it is found in the upper forest stratum, occupying the same zone as the White-crested Elaenia (*Elaenia albiceps*) (Sielfeld 1977). However, MMA consistently found it sally-striking (sensu Remsen and Robinson 1990) in the understory in 1977 at Nahuelbuta, at the northern end of the breeding range.

In winter, *C. parvirostris* extends its range outside and north of the beech forest. Habitats occupied by the species are more diverse at this time than during the breeding season, and its elevational range also increases. Goodall et al. (1946) noted that it can be found regularly in small numbers along the valleys and streams of the Andean pre-cordillera, in the coastal region, and in gardens of the cities of the Central Valley. The species may be found near small streams, where it perches low on bushes or weeds and sallies for passing insects in similar fashion to other small flycatchers (Wetmore 1926). Goodall et al. (1946), however, maintained that it is essentially arboreal, spending nearly all its time in treetop foliage, especially quillay (*Quillaja saponaria*) and maitén (*Maitenus boaria*) trees, and that it flies only occasionally and for short distances (presumably referring to the sallying noted by other observers). When insects are scarce in the mountains, it feeds on seeds of the maitén (Barros 1966); numbers of *C. parvirostris* are low in years when these seeds are few (Barros 1921). Jaffuel and Pirion (1928) reported large numbers in June at Valle de Marga-Marga (3301/7134), hunting for insects along the length of the valley. Housse (1925) noted this species feeding on small seeds at San Bernardo (3336/7043).

Our winter data, from San Manuel, Prov. Melipilla, indicate that *C. parvirostris* sally-strikes horizontally from low perches (typically 1.5–2.0

m) in bushes or small, defoliated trees. Espino (*Acacia cavens*) and the introduced American elm (*Ulmus americana*) are most commonly used, and the birds prefer perches on the outer positions and lower halves of the trees. In addition to sallies, individuals occasionally search live or dead leaves for insects. Sally-distance is variable, generally from 0.5 to 3 m. Occasional low flights are made; apparently the birds feed on flushed insects during these flights. The highest densities of *C. parvirostris* occurred in riparian forest with mixed native trees, although this species also was present in trees and bushes along field edges.

DISCUSSION

Colorhamphus parvirostris breeds primarily in *Nothofagus* forest along the eastern and western slopes of the Andes from the Tierra del Fuego archipelago north to the Coronel/Pichinahuel area. The species winters uncommonly in its breeding range and becomes fairly common in winter in regions of Chile north of the breeding range. North of Santiago, wintering individuals are more common along Andean slopes and valleys than in lowland, coastal areas, and the northern limit of the winter range appears to lie in Province Limarí. Autumn migration takes place primarily in April and early May, and spring migration in September and October. *Colorhamphus parvirostris* has been reported to have a breeding (Olrog 1963) and wintering (Meyer de Schauensee 1966, 1970) range in Argentina far beyond the Patagonian region reported here. These assertions are apparently the result of misinterpretation of Zotta's (1939) nesting record and the accretion of subsequent errors. Olrog (1963) cited Buenos Aires as the nest locality reported by Zotta, an error repeated by Johnson (1967), who nevertheless doubted the validity of the record. Meyer de Schauensee (1966, 1970) corrected these statements; however, he included Buenos Aires in the *winter* range of *C. parvirostris,* and this error was repeated by Sibley and Monroe (1990). We accept neither these assertions nor the discredited (Hellmayr 1932) report of Darwin (1839) that he collected this species along the banks of the Río de La Plata, and we note that Narosky and Di Giacomo (1993) reached the same conclusion. We were able to locate valid Argentine records only from the Patagonian provinces of Neuquén, Río Negro, Chubut, Santa Cruz, and Tierra del Fuego.

As mentioned above, several nesting records of *C. parvirostris* have been challenged as not pertaining to this species. Hellmayr (1932) considered the identification of the nests found by Pässler (1922) to be questionable, because of the lack of an accompanying specimen and presumably due to the great distance between Pässler's Coronel locality and the then-known Chilean nesting range (reported by Hellmayr as Isla Hoste and Tierra del Fuego). However, the nests and eggs described by Pässler

do not differ substantially from other nests and eggs reported for this species, and the three nests found at Pichinahuel (Marín et al. 1989) confirm that *C. parvirostris* nests as far north as the Concepción area. Thus, we consider these nest records valid. Johnson (1967) rejected Zotta's (1939) nest record from Buenos Aires as too far from the normal breeding range of the species and too divergent in nest description and egg size from a nest in Chilean Tierra del Fuego, and Casas et al. (1990) likewise questioned whether Zotta's nest pertained to *C. parvirostris.* We have shown that Johnson misreported the nesting locality, and we fail to see that the eggs reported by Zotta (white with small chestnut-reddish spots, primarily on the larger end; 19 × 14 mm) differ greatly from others of this species. Although the nest differed in its elongated form from other records (see photograph in Zotta 1939), the measurements, placement, and materials of the nest are similar to those of Pässler (1922), Marín et al. (1989), and others, as outlined previously. We note that the form of the nest was probably influenced by the substrate ("arbustos de retama" [broom]). Therefore, we believe Zotta's nest record to be valid.

The overlap of breeding and wintering ranges exhibited by *C. parvirostris* is typical of Chilean migrants in general. Of some 37 migrant passerine species breeding in Chile, for instance, only a handful (e.g., the White-browed Ground-Tyrant [*Muscisaxicola albilora*]) appear to vacate the country during the austral winter (Fjeldså and Krabbe 1990; Chesser, unpubl. data). Most Chilean migrants, such as *C. parvirostris,* leave the southern part of their breeding range in winter or the northern part of their wintering range in summer, but may be found throughout the year in other parts of their range. Still others, such as the Austral Thrush (*Turdus falcklandii magellanicus*) may undergo seasonal shifts in population density, with little change in range (Chesser, unpubl. data).

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Appendix 1

Specimens of *Colorhamphus parvirostris* for Which Date and Locality of Collection Are Available, Arranged by Month and Day of Collection

Date	Locality[a]	Latitude (S)	Longitude (W)	Collection[b]
Jan. 1938	ARG: Rio Negro, Lago Hess [ca 800 m]	41°22′	71°43′	MACN
Jan. 1977	CHL: Antarctica, Isla Hoste, Seno Ponsonby	55°05′	68°50′	[c]
2 Jan. 1898	CHL: Magallanes, Punta Arenas [sea level]	53°09′	70°55′	FMNH
3 Jan. 1898	CHL: Magallanes, Punta Arenas [sea level]	53°09′	70°55′	AMNH
3 Jan. 1898	CHL: Magallanes, Punta Arenas [sea level]	53°09′	70°55′	FMNH
3 Jan. 1898	CHL: Magallanes, Punta Arenas [sea level]	53°09′	70°55′	FMNH
17 Jan. 1990	ARG: Chubut, Lago Vintter [925 m]	43°56′	71°40′	KUMNH
17 Jan. 1990	ARG: Chubut, Lago Vintter [925 m]	43°56′	71°40′	KUMNH
17 Jan. 1990	ARG: Chubut, Lago Vintter [925 m]	43°56′	71°40′	KUMNH
Feb. 1937	ARG: Neuquén, Sierra de Pilpil, 1500 m	ca 40°58′	ca 71°30′	MACN
Feb. 1939	ARG: Santa Cruz, Lago San Martín [285 m]	48°52′	72°40′	MACN
Feb. 1939	ARG: Santa Cruz, Lago San Martín [285 m]	48°52′	72°40′	MACN
4 Feb. 1962	CHL: Coihaique, Coihaique Alto, 650 m	45°29′	71°36′	CAFB
13 Feb. 1983	CHL: Magallanes, I. Capitán Aracena, B. Morris	54°15′	71°00′	FMNH
17 Feb. 1984	CHL: Osorno, Refugio de la Picada [505 m]	41°04′	72°48′	FMNH
Mar. 1895	ARG: Tierra del Fuego, Lapataja [sea level]	54°53′	68°10′	[d]
Mar. 1895	CHL: Antarctica, B. Tekenika, False Cape Horn	55°43′	68°05′	[d]
Mar. 1928?	CHL: Malleco, Valle de Angol, Angol [72 m]	37°48′	72°43′	MHNV
4 Mar. 1972	ARG: Neuquén, M. Redondo, Isla Victoria [800 m]	40°56′	71°33′	PROBBAS
21 Mar. 1939	CHL: Llanquihue, Puerto Montt [sea level]	41°28′	72°57′	CM
23 Mar. 1981	CHL: Chiloé, Laguna Pío-Pío [ca 80 m]	42°49′	73°34′	WFVZ
25 Mar. 1981	CHL: Chiloé, Laguna Pío-Pío [ca 80 m]	42°49′	73°34′	WFVZ
28 Mar. 1981	CHL: Chiloé, Laguna Pío-Pío [ca 80 m]	42°49′	73°34′	WFVZ
11 Apr. 1895	CHL: Ñuble, Llohué [ca 200 m]	36°20′	72°24′	BMNH

Appendix 1
Continued

Date	Locality[a]	Latitude (S)	Longitude (W)	Collection[b]
17 Apr. 1971	CHL: Magallanes, Fuerte Bulnes, 30 m	53°37′	70°56′	USNM
17 Apr. 1971	CHL: Magallanes, Fuerte Bulnes, 30 m	53°37′	70°56′	USNM
24 Apr. 1971	ARG: Tierra del Fuego, Bahía Buen Suceso	54°47′	65°15′	USNM
26 Apr. 1921	CHL: Valparaíso, Concón [sea level]	32°55′	71°31′	USNM
27 Apr. 1921	CHL: Valparaíso, Concón [sea level]	32°55′	71°31′	USNM
May 1854	CHL: Santiago, Santiago [500 m]	33°27′	70°40′	MNHN
3 May 1923	CHL: Cachapoal, Baños de Cauquenes [ca 600 m]	34°15′	70°34′	FMNH
4 May 1924	CHL: C. Caro, Valle de Nilahue [ca 100 m]	34°34′	71°48′	LACM
9 May 1910	CHL: Cautín, Temuco [113 m]	38°44′	72°36′	BMNH
15 May 1940	CHL: Valdivia, Corral [sea level]	39°52′	73°26′	[e]
16 May 1943	CHL: Concepción, San Pedro [13 m]	36°52′	73°05′	CAFB
20 May 1903	CHL: Concepción [9 m]	36°50′	73°03′	AMNH
20 May 1903	CHL: Concepción [9 m]	36°50′	73°03′	AMNH
20 May 1910	CHL: Cautín, Temuco, Pelal [92 m]	38°50′	72°40′	BMNH
21 May 1925	CHL: Los Andes, Los Andes [816 m]	32°50′	70°37′	AMNH
Jun. 1865	CHL: Santiago, vicinity of Santiago [ca 500 m]	ca 33°27′	ca 70°40′	USNM
Jun. 1894	CHL: Concepción, Tumbes	36°40′	73°08′	[d]
Jun. 1939	CHL: Curicó, Curicó [ca 225 m]	34°59′	71°14′	MLP
Jun. 1939	CHL: Talca, Camarico [ca 100 m]	35°13′	71°25′	MLP
1 Jun. 1914	CHL: Chiloé, Ancud [109 m]	41°52′	73°50′	AMNH
14 Jun. 1932	CHL: Santiago, Las Condes [ca 700 m]	33°22′	70°31′	BMNH
14 Jun. 1932	CHL: Santiago, Las Condes, [ca 700 m]	33°22′	70°31′	BMNH
14 Jun. 1932	CHL: Santiago, Las Condes, [ca 700 m]	33°22′	70°31′	BMNH
17 Jun. 1939	CHL: Concepción, Concepción [9 m]	36°50′	73°03′	CAFB
21 Jun. 1894	CHL: Valparaíso, San Alfonso [sea level]	32°37′	71°21′	[f]
21 Jun. 1894	CHL: Valparaíso, San Alfonso [sea level]	32°37′	71°21′	[f]

Appendix 1
Continued

Date	Locality[a]	Latitude (S)	Longitude (W)	Collection[b]
21 Jun. 1907	CHL: Cautín, Maquehue [115 m]	38°46′	72°37′	BMNH
25 Jun. 1895	CHL: Cachapoal, Santa Teresa (Requínoa)	34°26′	70°50′	BMNH
26 Jun. 1894	CHL: Valparaíso, San Alfonso [sea level]	32°37′	71°21′	BMNH
26 Jun. 1894	CHL: Valparaíso, San Alfonso [sea level]	32°37′	71°21′	BMNH
27 Jun. 1981	CHL: Limarí, Punitaqui, 300 m	30°50′	71°15′	WFVZ
28 Jun. 1961	ARG: Río Negro, El Bolsón [384 m]	41°58′	71°31′	LACM
28 Jun. 1981	CHL: Limarí, Huilmo, 800 m	30°50′	71°05′	WFVZ
28 Jun. 1981	CHL: Limarí, Huilmo, 800 m	30°50′	71°05′	WFVZ
29 Jun. 1981	CHL: Limarí, Huilmo, 800 m	30°50′	71°05′	WFVZ
Jul. 1934	CHL: Cordillera, Valle del Maipo, 1200 m	33°37′	71°39′	MCZ
Jul. 1934	CHL: Cordillera, Valle del Maipo, 2000 m	33°37′	71°39′	MCZ
Jul. 1934	CHL: Cordillera, Valle del Maipo, 2000 m	33°37′	71°39′	MCZ
Jul. 1934	CHL: Cordillera, Valle del Maipo, 2000 m	33°37′	71°39′	MACN
2 Jul. 1981	CHL: Limarí, Las Ramadas, 1500 m	31°02′	70°36′	WFVZ
2 Jul. 1981	CHL: Limarí, Las Ramadas, 1500 m	31°02′	70°36′	WFVZ
4 Jul. 1959	CHL: Melipilla, Alhué	poss. 34°02′	poss. 71°06′	WFVZ
4 Jul. 1959	CHL: Melipilla, Alhué	poss. 34°02′	poss. 71°06′	WFVZ
4 Jul. 1981	CHL: Limarí, Huilmo, 800 m	ca 30°50′	ca 71°05′	WFVZ
10 Jul. 1981	CHL: Limarí, Huilmo, 800 m	ca 30°50′	ca 71°05′	WFVZ
11 Jul. 1939	CHL: Concepción, Concepción [9 m]	36°50′	73°03′	CAFB
13 Jul. 1925	CHL: Los Andes, Los Andes, 1500 m	32°50′	70°37′	FMNH
14 Jul. 1939	CHL: Curicó, Llico [sea level]	34°46′	72°05′	LACM
18 Jul. 1922	CHL: Los Andes, Los Andes, 840 m	32°50′	70°37′	LACM
19 Jul. 1921	CHL: Los Andes, Los Andes, 840 m	32°50′	70°37′	LACM
20 Jul. 1945	CHL: Linares, Linares [ca 100 m]	35°51′	71°36′	MACN

Appendix 1
Continued

Date	Locality[a]	Latitude (S)	Longitude (W)	Collection[b]
Aug. 1935	CHL: Valparaíso, Quinteros [sea level]	32°47′	71°32′	MLP
Aug. 1938	CHL: Valparaíso, Quinteros [sea level]	32°47′	71°32′	MCZ
Aug. 1938	CHL: Valparaíso, Quinteros [sea level]	32°47′	71°32′	MCZ
Aug. 1938	CHL: Valparaíso, Quinteros [sea level]	32°47′	71°32′	FML
Aug. 1938	CHL: Valparaíso, Quinteros [sea level]	32°47′	71°32′	MLP
Aug. 1938	CHL: Valparaíso, Quinteros [sea level]	32°47′	71°32′	MLP
Aug. 1938	CHL: Valparaíso, Quinteros [sea level]	32°47′	71°32′	MLP
Aug. 1938	CHL: Valparaíso, Quinteros [sea level]	32°47′	71°32′	BMNH
Aug. 1938	CHL: Valparaíso, Quinteros [sea level]	32°47′	71°32′	BMNH
Aug. 1984	CHL: Limarí, El Palomo [ca 1700 m]	ca 30°46′	ca 71°10′	WFVZ
Aug. 1984	CHL: Limarí, El Palomo [ca 1700 m]	ca 30°46′	ca 71°10′	WFVZ
Aug. 1984	CHL: Limarí, El Palomo [ca 1700 m]	ca 30°46′	ca 71°10′	WFVZ
Aug. 1984	CHL: Limarí, El Palomo [ca 1700 m]	ca 30°46′	ca 71°10′	WFVZ
Aug. 1984	CHL: Limarí, El Palomo [ca 1700 m]	ca 30°46′	ca 71°10′	WFVZ
Aug. 1984	CHL: Limarí, El Palomo [ca 1700 m]	ca 30°46′	ca 71°10′	WFVZ
Aug. 1984	CHL: Limarí, near Punitaqui [ca 500 m]	30°50′	71°05′	WFVZ
1 Aug. 1952	CHL: Valparaiso, Quinteros [sea level]	32°47′	71°32′	YPM
1 Aug. 1952	CHL: Valparaiso, Concón [sea level]	32°55′	71°31′	YPM
1 Aug. 1952	CHL: Cachapoal, Rancagua [499 m]	34°10′	70°45′	YPM
3 Aug. 1914	CHL: Magallanes, Punta Arenas [sea level]	53°09′	70°55′	AMNH
4 Aug. 1940	CHL: Cordillera, Rio Colorado, 1000 m	33°27′	70°40′	MCZ
10 Aug. 1952	CHL: San Antonio, El Quisco [sea level]	33°24′	71°42′	UMMZ
10 Aug. 1981	CHL: Chacabuco, Colina, El Portezuelo, 650 m	33°20′	70°42′	WFVZ
11 Aug. 1920	CHL: Los Andes, Río Blanco, 1550 m	32°55′	70°19′	AMNH

Appendix 1
Continued

Date	Locality[a]	Latitude (S)	Longitude (W)	Collection[b]
11 Aug. 1920	CHL: Los Andes, Río Blanco, 1550 m	32°55′	70°19′	AMNH
11 Aug. 1920	CHL: Los Andes, Río Blanco, 1550 m	32°55′	70°19′	LACM
12 Aug. 1920	CHL: Los Andes, Río Blanco, 1550 m	32°55′	70°19′	AMNH
12 Aug. 1920	CHL: Los Andes, Río Blanco, 1550 m	32°55′	70°19′	LACM
12 Aug. 1923	CHL: Los Andes, Los Andes, 840 m	32°50′	70°37′	LACM
13 Aug. 1969	CHL: Melipilla, Malvilla	33°44′	71°13′	WFVZ
15 Aug. 1920	CHL: Los Andes, Río Blanco, 1540 m	32°55′	70°19′	LACM
15 Aug. 1924	CHL: Los Andes, Río Blanco, 1540 m	32°55′	70°19′	FMNH
15 Aug. 1924	CHL: Los Andes, Río Blanco, 1560 m	32°55′	70°19′	UMMZ
15 Aug. 1947	CHL: Santiago, Baños de Colina [600 m]	33°11′	70°36′	MCZ
20 Aug. 1965	CHL: Talagante, Talagante [ca 500 m]	33°40′	70°56′	MNHN
23 Aug. 1916	CHL: Santiago, Apoquindo [1000 m]	33°24′	70°32′	AMNH
24 Aug. 1916	CHL: Santiago, Apoquindo [1000 m]	33°24′	70°32′	AMNH
24 Aug. 1931	CHL: Santiago, Las Condes [ca 700 m]	33°22′	70°31′	BMNH
25 Aug. 1932	CHL: Santiago, La Dehesa [875 m]	33°22′	70°33′	FMNH
25 Aug. 1932	CHL: Santiago, Santiago [500 m]	33°27′	70°40′	FMNH
26 Aug. 1940	CHL: Curicó, Llico [sea level]	34°46′	72°05′	LACM
30 Aug. 1910	CHL: Cautín, Maquehue [115 m]	38°46′	72°37′	AMNH
31 Aug. 1984	CHL: Limarí, Cerro Guaquilón	ca 30°50′	ca 71°05′	WFVZ
2 Sep. 1941	CHL: Llanquihue, Maullín [sea level]	41°38′	73°37′	LACM
5 Sep. 1969	ARG: Río Negro, El Bolsón [384 m]	41°58′	71°31′	LSUMZ
6 Sep. 1962	ARG: Río Negro, El Bolsón [384 m]	41°58′	71°31′	FML
12 Sep. 1944	CHL: Ñuble, Atacalco [ca 500 m]	36°50′	71°47′	CAFB
21 Sep. 1961	ARG: Río Negro, El Bolsón [384 m]	41°58′	71°31′	AMNH
27 Sep. 1940	CHL: Valdivia, Enco [ca 200 m]	39°53′	72°11′	[e]

Appendix 1
Continued

Date	Locality[a]	Latitude (S)	Longitude (W)	Collection[b]
27 Sep. 1940	CHL: Valdivia, Enco [ca 200 m]	39°53′	72°11′	[e]
12 Oct. 1961	CHL: Cordillera, Valle de Engorda, 2700 m	34°10′	69°50′	UMMZ
10 Nov. 1938	ARG: Río Negro, Lago Hess [ca 800 m]	41°22′	71°43′	MACN
24 Dec. 1922	CHL: Chiloé, Quellón [sea level]	43°07′	73°37′	FMNH
28 Dec. 1897	CHL: Magallanes, Punta Arenas [sea level]	53°09′	70°55′	AMNH

[a] Localities are arranged as follows: country, province, specific locality, elevation. The new province system was used for Chilean localities. Elevations in brackets were taken from gazetteers, the others from specimen labels.

[b] AMNH = American Museum of Natural History; BMNH = British Museum (Natural History); CAFB = Colección de Aves de Francisco Behn; CM = Camegie Museum; FML = Fundación Miguel Lillo; FMNH = Field Museum of Natural History; KUMNH = Univ. of Kansas Museum of Natural History; LACM = Los Angeles County Museum; LSUMZ = Louisiana State Univ. Museum of Natural Science; MACN = Museo Argentino de Ciencias Naturales; MCZ = Museum of Comparative Zoology; MHNV = Museo Historia Natural El Vergel; MNHN = Museo Nacional Historia Natural Santiago; MLP = Museo de La Plata; PROBBAS = Programa de Biologia Basica y Aplicada Subtropical; UMMZ = Univ. of Michigan Museum of Zoology; USNM = National Museum of Natural History; WFVZ = Western Foundation of Vertebrate Zoology; YPM = Yale Peabody Museum.

[c] Specimen data from Sielfeld (1977).

[d] Specimen data from Schalow (1898).

[e] Specimen data from Olrog (1948).

[f] Specimen data from Hellmayr (1932).

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TRADE-OFFS AND CONSTRAINTS ON EASTERN KINGBIRD PARENTAL CARE

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ABSTRACT.—Ten Eastern Kingbird (*Tyrannus tyrannus*) nests were observed for 97 h to determine age-related changes in parental care and to identify possible trade-offs and constraints on feeding, brooding, and vigilant behavior. Feeding rate (trips/h) was related positively to nestling age and brood size, but related negatively to amount of time spent vigilant. Per capita nestling feeding rates (trips/nestling/h) were affected most strongly and negatively by brood size, precipitation, and time spent vigilant. Time spent brooding declined as nestlings aged and as air temperature rose, whereas the amount of time spent shading nestlings varied only (inversely) with cloud cover. Vigilance time averaged about 20% of each hour, was independent of age and brood size, but was related negatively to amount of time spent in nestling maintenance (brooding plus shading), the number of feeding trips made to nests, and nest visibility. Weather had major influences on feeding and brooding behaviors, but regardless of other factors, kingbirds appear to reserve time for vigilance. Parental behavior thus reflects the action of a large number of factors that require compromises in the apportionment of time to the feeding, maintenance, and protection of young. *Received 10 Sept. 1993, accepted 20 Feb. 1994.*

Parental behaviors, such as feeding rates, often change predictably over the course of the nesting cycle (Bedard and Meunier 1983, Moreno 1987), but considerable variation in parental behavior may result from the action of unpredictable environmental factors. Variation in parental care due to weather is often of great ecological significance, and only by documenting and identifying the causes of variation can its importance be appreciated (Johnson and Best 1982, Wittenberger 1982). Furthermore, studies of how parental behavior changes throughout the nesting cycle provides information as to whether trade-offs exist among parental behaviors (Breitwisch et al. 1986, Grundel 1987, Haggerty 1992) and when critical periods in development occur (Morehouse and Brewer 1968).

Eastern kingbirds (*Tyrannus tyrannus*) are single-brooded and normally lay a clutch of three or four eggs (Murphy 1983a, Blancher and Robertson 1985a). Predation is the major cause of nest mortality (Murphy 1983b, Blancher and Robertson 1985b), but low temperatures and/or precipitation have negative impacts on nestling growth and fledging success (Murphy 1983c, Hayes and Robertson 1989). Here we document major components of parental care vary with nestling age and brood size, identify environmental sources of variation in parental care, and describe trade-offs that exist among parental behaviors.

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STUDY AREA AND METHODS

We conducted this study during June and July 1989 in the Charlotte Valley, Delaware Co., New York. The main study area was near Hartwick College's Pine Lake Biological Field Station, between the towns of Davenport and West Davenport. Habitats within the area are mainly a mixture of pastures, hedgerows and riparian environments. See Bischoff and Murphy (1993) for a more complete description of the area. All nests were found prior to egg-laying and were followed closely until laying was complete. We therefore knew the true clutch size for each nest (6 clutches of 3 eggs, 3 of 4 eggs and 1 of 2 eggs). Due to the failure of some eggs to hatch, and our desire to maintain a distribution of brood sizes similar to the original clutch sizes, Murphy transferred one or two nestlings into several nests within 24 to 48 h after hatching. Nestlings within a brood never differed in age by more than one day. Our observations are based on data from five broods of three young, three broods of four, and two broods of two. Rosa was not informed of brood sizes or nestling ages in order to keep observations unbiased. Observations at (usually) trios of nests with nestlings of the same age alternated between morning (before 11:00 EST), midday (11:00 to 13:00 EST) and afternoon (after 13:00 EST) on successive days. Observations at the same nest are not statistically independent. Conceivably, nests on low or high quality territories or nests tended by pairs with different levels of experience might produce spurious results. We attempted to minimize this potential problem by making observations at each nest at different times of day and over a range of weather conditions. Each observation period (N = 43) was treated as a single observation, based on the two (sometimes three) hours over which Rosa collected data. Our analysis is thus based on 97 h of observations from 10 nests.

Parental behaviors were monitored either from a blind located about 30 m from the nest or from a parked vehicle at the edge of roads. Using binoculars, Rosa observed nests between days 2 and 14 of the nestling period (hatching = 1). She collected data on the number of feeding trips and time spent brooding, chasing predators, shading young, and being vigilant. We did not analyze chasing time because little time was spent on this behavior. Time of day was recorded as the midpoint of the observation period. We included several nest sites characteristics in the analysis, including height (meters above ground), distance from the canopy edge (meters), and shading on a scale of 0 (no shading) to 4 (complete cover). Weather variables monitored during the observation period included air temperature, wind speed, precipitation and cloud cover. Rosa recorded each variable 30 minutes after observations began and then at hourly intervals until the observation period ended. Air temperature was measured with a shaded mercury thermometer. Other weather variables were estimated on a scale of 0 to 4. Scores of 0 were given to each variable when no wind, rainfall, or cloud cover was present. Conversely, observation periods with strong winds, heavy precipitation, and complete cloud cover were assigned values of 4.

We defined brooding as occurring when the female settled down on the nest and covered the nestlings. Shading females stood over the nestlings with wings spread to shield them from the sum. Nest attendance was the total time spent brooding and shading young. We defined a vigilant bird to be one that perched attentively in the vicinity of the nest, scanned the area while its mate was away from the nest, and did not feed either itself or the nestlings. Given that the birds were not individually marked, we did not attempt to separate feeding trips according to sex of the parent.

With the exception of feeding rates, we expressed all behaviors as a percentage (arcsine-transformed) of the total min of observation. We analyzed feeding rate as either the total number of trips/h or as the number of trips/nestling/h (=per capita feeding rate). Both the

TABLE 1

RESULTS OF THE MULTIPLE REGRESSION ANALYSIS OF FEEDING RATE (TRIPS/H) FOR KINGBIRD PAIRS IN 1989

Variable	Correlation coefficient (r)	Standardized regression coefficient	Type I F	Type III F
Log (age)	0.623[d]	3.848	46.82[d]	10.53[c]
Precipitation	−0.541[d]	−1.534	9.14[c]	3.42[a]
Nest attendance	−0.521[d]	−0.117	2.33	3.32[a]
Brood size	0.448[c]	1.891	14.42[d]	7.22[c]
Vigilance	−0.339[b]	−0.049	10.81[c]	10.81[c]
Model R^2 = 69.3%, F = 16.70, df = 5, 37, $P < 0.001$				

[a] $0.05 < P < 0.10$, [b] $P < 0.05$; [c] $P < 0.01$; [d] $P < 0.001$; all others not significant.

total and per capita feeding rates were roughly normally distributed. Nestling age was logarithmically transformed in analyses of feeding rate.

We used regression analyses (simple linear and multiple regression) to identify the factors underlying variation in parental behavior. We first examined the strength of the univariate relationships between each dependent variable and all the independent variables. Other behaviors were included as independent variables to examine the potential for trade-offs in parental activities. Variables that were associated significantly ($P < 0.05$) with the dependent variable were then entered into a multiple regression analysis in a sequence corresponding to the strengths of their univariate relationships. We then plotted the residuals against the remaining variables to check for additional relationships. If any were found, the variables were then added to the model. Our objective was to explain the maximum amount of variation in each dependent variable, with the provision that all predictor variables make significant, independent contributions. To assess the significance of each variable, we used the F-values based on the type III sums of squares (SS). Type I SS reflect the impact of each variable as it enters the model, but type III SS measure the significance of each variable only after all the other variables have been entered into the regression model (SAS 1985). For a variable to be retained in the model, we required that its effects remain statistically significant when it was the last variable entered in the model, which meant that the variable had to have a significant type III SS. After the final regression models for feeding rates were determined, we tested for effects of either parental or territory quality by performing an analysis of variance (ANOVA) on the residuals. Unless otherwise noted, significance was established at $P < 0.05$.

RESULTS

Feeding rates.—Age entered the regression first, followed by rainfall, nest attendance, brood size, and vigilance (Table 1). Feeding rate also exhibited significant univariate correlations with cloud cover ($r = -0.373$, $P = 0.01$) and nest cover ($r = 0.442$, $P < 0.01$), but neither had significant type III sums of squares in the regression and were dropped from the model. Thus, feeding rate was positively related to age and brood size but tended to decline as the amount of time spent vigilant increased. The

TABLE 2

RESULTS OF THE MULTIPLE REGRESSION ANALYSIS OF PER CAPITA NESTLING FEEDING RATE (TRIPS/NESTLING/H) FOR KINGBIRDS IN 1989

Variable	Correlation coefficient (r)	Standardized regression coefficient	Type I F	Type III F
Log (age)	0.606[d]	1.051	34.33[d]	4.79[b]
Precipitation	−0.506[d]	−0.935	5.61[b]	7.74[c]
Nest attendance	−0.482[d]	−0.022	1.12	4.25[b]
Brood size	−0.186	−1.012	8.55[c]	12.61[d]
Vigilance	−0.136	−0.038	6.77[c]	6.77[c]
Model R^2 = 60.4%, F = 11.28, df = 5, 37, $P < 0.0001$				

[a] $0.05 < P < 0.10$; [b] $P < 0.05$; [c] $P < 0.01$; [d] $P < 0.001$; all others not significant.

five-variable model accounted for roughly 70% of the variation in feeding rate. The ANOVA comparing the residual variation among the 10 pairs was not significant (F = 1.30; df = 9, 33; P = 0.27). Thus, none of the unexplained variation appeared to be associated with differences in either parental and/or territory quality.

Although precipitation and nest attendance failed to make significant contributions when entered last (type III SS, Table 1), both were significant ($P < 0.05$) when entered at the last step if the other variable was excluded from the model. In addition, both four variable models explained identical amounts (R^2 = 0.665) of the variation in feeding rate. The failure of either variable to achieve significance when both were incorporated in the same model probably stems from the fact that attendance and precipitation were positively correlated (r = 0.440, P = 0.003). Given that each alone made significant contributions and that our inability to determine which variable was of primary importance, we chose to retain both in the final model (Table 1).

Per capita nestling feeding rates (trips/nestling/h) were correlated significantly with only three of the five variables used in the analysis of total trips/h. In addition to age, precipitation, and nest attendance (Table 2), per capita feeding rates varied with date (r = 0.302, P = 0.05) and cloud cover (r = −0.559, $P < 0.001$), but both variables failed to remain significant in the multiple regression and were dropped from the model. Instead, an examination of the residuals after accounting for age, precipitation, and nest attendance suggested that per capita feeding rates were negatively related to brood size and time spent vigilant. Both of the latter variables were, therefore, entered and retained in the final model and made large contributions (Table 2). Brood size became the most important

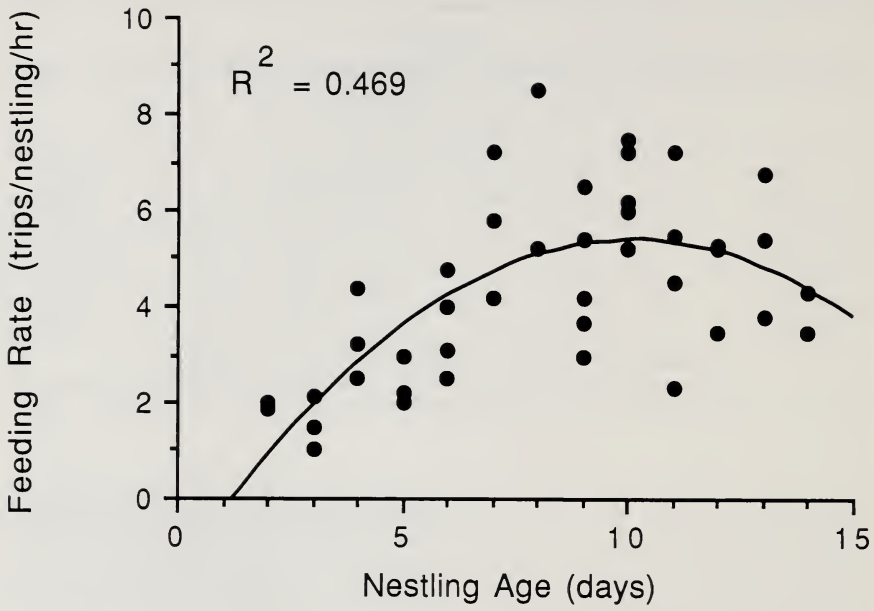

FIG. 1. Per capita nestling feeding rates (trips/nestling/h) plotted against age. The line in the plot is the second-order polynomial described by the formula, FEEDING RATE = $-1.63 + 1.387(\text{AGE}) - 0.068(\text{AGE}^2)$. Each point represents the average calculated over either a two- or three-h observation period.

determinant of per capita feeding rate, followed by precipitation and vigilance. Overall, the model accounted for 60% of the variation in the number of feeding trips/nestling/h. Residual variation was again unrelated to differences among pairs or territories ($F = 1.0$; df = 9, 33; $P = 0.46$).

That nestling age was of reduced importance in explaining per capita feeding rate (Table 2) was unexpected. The apparent reason was that per capita feeding rate appeared to peak near 10 days of age (Fig. 1). A second-order polynomial explained 46.9% of the variation ($P < 0.001$) in feeding rate. Our results are strikingly similar to data collected by Morehouse and Brewer (1968) from a Michigan population of kingbirds (Fig. 2). Based on the average feeding rate at each age, second-order polynomials accounted for 67.8% and 66.2% of the variation in per capita nestling feeding rate in New York and Michigan, respectively (Fig. 2). In both populations, the predicted maximum feeding rate approached 5.5 trips/nestling/h at either 10 (New York) or 12 (Michigan) days of age. Given this, we reanalyzed per capita feeding rates using the second-order polynomial of age, along with precipitation, nest attendance, brood size,

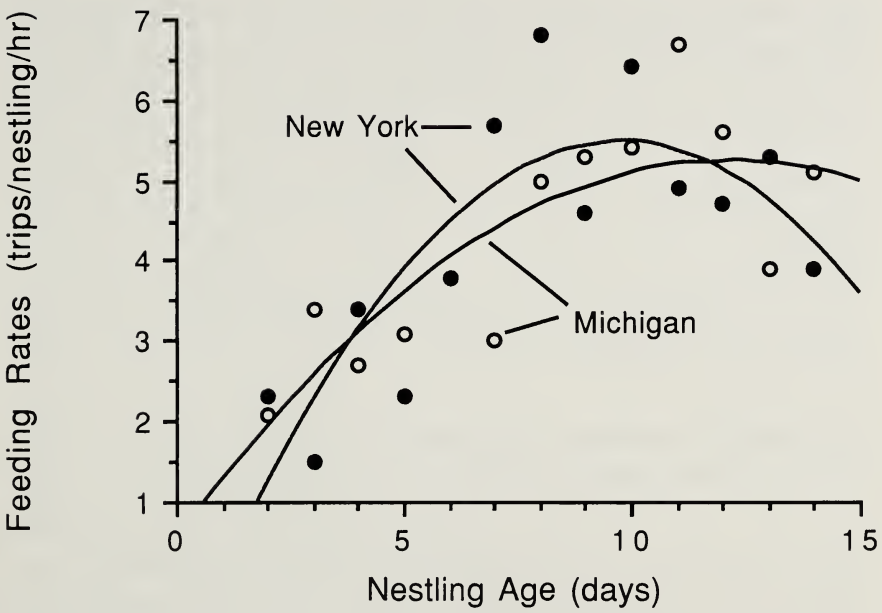

FIG. 2. Average per capita nestling feeding rates by nestling age for the New York study population (solid dots) and a Michigan kingbird population (open circles; from Morehouse and Brewer 1968). Each point represents the mean of 7.5 ± 1.9 h and 7.5 ± 4.67 h of observation in New York and Michigan, respectively. Both curves are second-order polynomials and are described by the following equations: New York, RATE = −1.221 + 1.368(AGE) − 0.070(AGE^2), R^2 = 0.678, and Michigan, RATE = 0.523 + 0.774(AGE) − 0.036(AGE^2), R^2 = 0.662.

and vigilance. The explained variation increased slightly (R^2 = 62.4%; F = 11.28; df = 6, 36; $P < 0.001$), and all of the variables remained significant.

Nestling maintenance.—All analyses of brooding time excluded days 12–14 since kingbirds stopped brooding completely after day 10. Other than age, the other major correlates of brooding were weather variables. Brooding increased as cloud cover (r = 0.752) and precipitation (r = 0.624) increased and as temperatures fell (r = −0.564; df = 34 and $P <$ 0.001 for all three). Time spent shading (r = −0.362, $P < 0.02$) and total and per capita feeding rates also correlated negatively with time spent brooding (both $P < 0.001$), but the only factor to remain significant, once the affect of nestling age was taken into account, was mean temperature during the observation period (type III SS, F = 43.95, $P < 0.001$). Nestlings under 12 days of age were brooded more when temperatures were

TABLE 3

RESULTS OF THE MULTIPLE REGRESSION ANALYSIS OF TIME SPENT VIGILANT (MIN/H) AT NESTS BY KINGBIRDS IN 1989

Variable	Correlation coefficient (r)	Standardized regression coefficient	Type I F	Type III F
Nest cover	-0.455^{b}	-4.600	13.38^{c}	7.18^{b}
Feeding rate	-0.339^{a}	-1.157	1.52	7.12^{b}
Nest attendance	-0.176	-0.292	10.73^{b}	10.73^{b}
Model R^2 = 39.7%, F = 8.55, df = 3, 39, $P < 0.0002$				

$^{a}P < 0.05$; $^{b}P < 0.01$; $^{c}P < 0.001$; all others not significant.

low. Age and air temperature accounted for over 81.1% of the variation in time spent brooding (F = 69.74; df = 2, 32; $P < 0.001$).

The amount of time spent shading varied independently of age (r = 0.163, df = 41). On average, females shaded young for 6.3 min each hour, but variability was very high ($\bar{x} \pm$ SD for percentage of time spent shading 10.6 ± 21.00%). Shading increased when there was little cloud cover ($r = -0.398$, $P < 0.01$) but decreased as brooding time increased ($r = -0.362$, $P = 0.02$) or when air temperatures rose ($r = 0.313$, $P < 0.05$). Of these, only cloud cover remained significant when all three or a combination of any two of the variables was entered into a multiple regression. Plots of the residuals failed to show any trends with other variables. Thus, females shaded young on clear, sunny days.

Vigilance.—The amount of time spent vigilant varied independently of age (r = 0.108, df = 41) and averaged 11.4 min/h (19.0% of each hour ± 17.52%). Vigilance tended to be low when nest cover was high ($r = -0.455$, $P < 0.001$) and as the number of feeding trips/h increased ($r = -0.339$, $P < 0.005$). After entry of both variables into the model, we found that residual vigilance was negatively correlated with nest attendance (time spent brooding and shading). The three-variable model of nest cover, feeding rate, and nest attendance explained 40% of the variation in vigilance time (Table 3). After controlling for the effects of these three variables, we found that residual vigilance did not vary with brood size (Kruskal-Wallis test, H = 2.416).

DISCUSSION

Activity at the nest was affected by a wide range of factors, only some of which were predictable (e.g., age) or under parental control (e.g., brood size or nest cover). That feeding rates and brooding behavior varied with nestling age was not surprising and has been documented in this (More-

house and Brewer 1968) and other species (Bedard and Meunier 1983, Best 1977, Breitwisch et al. 1986, Grundel 1987, Johnson and Best 1982, Moreno 1987, Haggerty 1992). Morehouse and Brewer's (1968) and our studies agree in showing that maximum per capita nestling feeding rates average about 5.5 trips per nestling/h and that feeding rate declines towards the end of the nestling period. The decline is temporary, however, since feeding rate nearly doubles about one week after fledging occurs (Morehouse and Brewer 1968). Furthermore, we found that brood size greatly affected nestling feeding rates. Large broods received more feeding trips/h than small broods, but the increase was not sufficient to maintain equivalent rates of feeding to individual nestlings in large broods. Hence, young in large broods were fed less. Differences in parental and/or territory quality did not appear to have an impact on feeding rates since the residual variation from the multiple regressions of total and per capita feeding rates could not be partitioned among nests. This finding indicates that our results were not unduly influenced by conditions at particular nests.

On the other hand, parental behavior was influenced substantially by environmental factors. Precipitation caused feeding rates to drop and low temperatures forced females to brood young. Given that nest attendance was mainly a product of brooding behavior and that nest attendance was negatively correlated with per capita nestling feeding rates (Table 2), weather was clearly an important contributor to variation in the number of times individual nestings were fed. Low feeding rates during inclement weather no doubt resulted from the direct negative effects of precipitation on food availability (e.g., Bryant 1975, Davies 1977) and the indirect effects of low temperature on time spent brooding. This confirms an earlier report (Murphy 1983c) which showed that nestling kingbirds grew poorly and starved frequently when rainfall was high and temperatures were low. Females cannot simultaneously provide adequate food and brood young when weather deteriorates (see also Johnson and Best 1982 and Wittenberger 1982 for similar conclusions for other species). The trade-off between nestling feeding and maintenance suggests a hitherto neglected conflict that may have bearing on the evolution of clutch size. Open-cup nesting species such as kingbirds must surely expend much greater amounts of time and energy maintaining the thermal environment of their nests than do cavity-nesters. The smaller clutch sizes typical of open-cup nesting species (Lack 1968, Martin and Li 1992) may reflect simple constraints on feeding rate and time budgets during thermally stressful periods, rather than differences either in rates of nest predation (Lack 1968, Slagsvold 1982, Lima 1987) or adult survivorship (Martin and Li 1992) between open-cup and cavity nesters.

Finally, the multiple regression analysis of vigilance highlights another important trade-off. Two of the three factors affecting vigilance were other behaviors (nest attendance and per capita nestling feeding rate). Indeed, vigilance time was the second most important correlate of feeding rate (Table 1). Parents must sometimes apparently choose between feeding or guarding young. On the other hand, we found that brood size did not influence the amount of time spent vigilant once we controlled for the effects of parental behaviors and nest cover. This suggests that vigilance was maintained in large broods at the expense of food deliveries.

Kingbirds are known for their vigilant behavior (Smith 1966) and aggressive defense of their nest (Davis 1941, Blancher and Robertson 1982). Smith (1966) noted that males rarely left the nest unattended during female absences. Vigilance presumably improves long distance detection of predators which can then be attacked and kept from the vicinity of the nest. Hayes and Robertson (1989) found a (nonsignificant) trend for widowed female kingbirds to lose more nests to predators than mated pairs. Interestingly, we found that high nest cover was associated with reduced vigilance, suggesting that kingbirds were able to perceive the conspicuousness of their nests and act accordingly. Although in need of further study, the value of aggressiveness and vigilance for kingbirds seems clear. Sacrificing nestling feeding in large broods to maintain vigilance presumably reduces losses of entire broods. Kingbird nests that fail early in the nest cycle are usually replaced, but as the season progresses the probability of renesting following failure declines (Murphy 1983a). Thus, the decision to maintain vigilance over feeding in large broods seems appropriate, given that total nest loss has a much graver impact on seasonal reproductive success than does the loss of an individual nestling to starvation.

Our results show that parental behavior was dynamic and influenced not only by nestling food requirements (as reflected in the correlations with age and brood size) but also by the need to maintain a favorable nest microenvironment and predator-free space. Failure to perform either of the latter two functions may result in complete nest loss to exposure (Murphy 1985) or predation (Murphy 1983b). Consequently, "apparent" food shortage may result from trade-offs in parental behavior, which may have important consequences for the evolution of clutch size and/or nestling growth rate (Lima 1987, Martin 1991).

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DYNAMICS OF OVARIAN FOLLICLES IN BREEDING DUCKS

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Abstract.—I quantified ovarian rapid follicle growth (RFG) and regression of postovulatory follicles of Northern Pintails (*Anas acuta*), American Wigeon (*A. americana*), and Lesser Scaup (*Aythya affinis*) by a method that accounted for within-day variation in follicle size. Objective methods for identifying onset of RFG also are presented; this is crucial for accurate classification of breeding status. Duration of RFG was estimated as 4.2, 5.1, and 5.0 days for pintails, wigeon, and scaup, respectively; these are shorter than previously reported. Diameters of follicles at the beginning of RFG were estimated to be 8.2, 6.9, and 7.9 mm for pintails, wigeon, and scaup, respectively. For all species, RFG was linear, using follicle diameters, and exponential, using dry masses. Models of RFG and postovulatory follicle regression have practical value for calculating nest initiation dates, number of developing follicles, clutch size, renesting intervals, and daily energy and nutrient commitment to reproduction of collected breeding females. *Received 12 November 1993, accepted 20 April 1994.*

Rapid follicle growth (RFG) is the period from the time an ovarian follicle begins rapidly accumulating yolk until ovulation (see Lofts and Murton [1973] for descriptions of ovary structure and control). In ovaries of breeding birds, initiation of RFG of successive follicles is staggered in accordance with egg-laying interval. As a result, developing follicles have a distinct size hierarchy that corresponds to the order in which they will be ovulated. Postovulatory follicles are the follicle structures remaining after ovulation (Lofts and Murton 1973); they regress over time, resulting, similarly, in a size heirarchy within an ovary. Based on this information and assumptions about rates of egg laying, models of RFG and postovulatory regression through time can be developed.

Previous studies have described ovarian follicle growth based on changes in mean follicle size by day (e.g., Calverley and Boag 1977, Astheimer and Grau 1990, Alisauskas and Ankney 1992) but did not present model equations. No previous investigators presented continuous models of RFG or postovulatory follicle regression with predictive capabilities that could be used in subsequent studies.

My objective was to quantify ovarian follicle dynamics of Northern Pintails (*Anas acuta*; hereafter pintails), American Wigeon (*A. americana*; hereafter wigeon), and Lesser Scaup (*Aythya affinis*; hereafter scaup) by methods that accounted for within-day variation and objectively identified

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onset of RFG. I also present models that can be used to discern aspects of breeding biology from ovaries of collected females.

METHODS

Female pintails were collected in 1990 and 1991 at study sites on Yukon Delta National Wildlife Refuge (NWR) (61°26′N, 165°27′W) and Yukon Flats NWR (66°25′N, 149°59′W), Alaska. In 1991, female wigeon and scaup were collected on Yukon Flats NWR. Ovaries were removed and preserved in 10% formalin. In the laboratory, largest diameters in the plane of the stigma of preovulatory and postovulatory follicles were measured. Dry masses of preovulatory follicles were recorded. Because follicles preserved in formalin may be fixed in deformed shapes, dry masses of preovulatory follicles may be more accurate than diameters. However, analyses using diameters are advantageous because these measures are obtainable in the field or lab without additional processing.

Only laying females (i.e., those that had ovulated at least one follicle) were used as samples for modeling, because only those could have a general hierarchy assigned by day. Ovaries with follicles broken during collection or dissection were included only if the position in the hierarchy of the broken follicle was known with certainty. For late-layers with a gap in the follicle hierarchy, only large, developing follicles were used.

Within each ovary, follicles were assigned to a DAY, which was a rough estimate of the time before ovulation. For example, the largest follicle from each ovary was assigned DAY = 1, and it was assumed that it would have ovulated with 24 h. The second largest follicle was assigned DAY = 2, and so forth. Sample sizes by species and DAY are presented in Table 1. For these analyses, I assumed constant laying intervals of 24 h for all species (Alisauskas and Ankney 1992).

Rather than describe a rough growth curve based on mean follicle size for each DAY, I incorporated within-day variation in follicle sizes into continuous models. I corrected DAY (CORRDAY) for individual birds, using an adjustment based on that bird's largest follicle dry mass (DRY) relative to the range in mass between the smallest DAY 1 follicle (SMLFOLL) of the species (Table 1) and an estimate of the individual's follicle mass at ovulation (LRGFOLL). LRGFOLL was either (1) dry mass of the individual's oviductal egg yolk or (2) average yolk dry mass from a sample of oviductal and laid eggs. The former was used, when possible, to account for variation in egg composition among individuals, which is greater than variation within clutches (Duncan 1987). Thus, CORRDAY estimated time before ovulation for the largest follicle of each individual as: CORRDAY = (LRGFOLL − DRY)/(LRGFOLL − SMLFOLL). For other follicles of each individual, CORRDAY was calculated by adding DAY for each follicle and CORRDAY from the largest follicle.

CORRDAY for the largest postovulatory follicle of each ovary (i.e., days after ovulation) was estimated using the correction for developing follicles: CORRDAY = 1 − (LRGFOLL − DRY)/(LRGFOLL − SMLFOLL). Because postovulatory follicle diameters were subject to more measurement error, CORRDAY based on preovulatory follicles likely was more accurate than deriving a correction factor based on postovulatory follicle sizes.

I used an iterative approach to quantify beginning of RFG for each species. First, I used linear regressions to describe relationships between CORRDAY and follicle diameter for data sets consisting of (1) follicles clearly before RFG (i.e., CORRDAY $\geq$ 6.0) and (2) follicles definitely in RFG (i.e., CORRDAY $<$ 3.5). Exclusion of that range of points avoided using data near the beginning of RFG for all species (Fig. 1). In the second iteration, separate linear regressions were used to describe data less and greater than CORRDAY at the intersection of models from the first iteration. The intersection of models from the second

TABLE 1
OVARIAN FOLLICLE SIZES OF BREEDING DUCKS

Day[a]		Northern Pintail		American Wigeon		Lesser Scaup	
		Diameter (mm)	Dry mass (g)	Diameter (mm)	Dry mass (g)	Diameter (mm)	Dry mass (g)
1	Range	26.3–33.4	4.56–7.80	28.3–34.5	5.63–8.18	30.8–35.6	7.27–10.63
	Mean	29.6	6.32	31.4	6.94	33.4	8.71
	N	42	40	11	11	15	15
2	Range	20.1–28.4	1.94–5.37	22.7–28.5	2.95–5.66	26.7–30.8	4.12–6.19
	Mean	24.1	3.43	26.2	4.27	28.8	5.27
	N	42	42	10	10	14	14
3	Range	14.4–23.2	0.65–2.62	17.8–23.3	1.30–2.75	18.6–24.7	1.50–3.93
	Mean	17.8	1.38	20.5	2.03	22.0	2.55
	N	41	41	8	8	14	14
4	Range	9.3–16.3	0.13–1.06	11.0–18.9	0.27–1.43	11.4–18.5	0.25–1.24
	Mean	12.0	0.42	14.6	0.78	15.5	0.81
	N	34	31	9	8	15	15
5	Range	6.0–11.8	0.01–0.34	7.6–14.4	0.07–0.57	8.2–13.2	0.06–0.40
	Mean	8.1	0.10	10.0	0.24	10.5	0.20
	N	26	21	7	6	13	12
6	Range	5.3–8.2	0.01–0.09	5.9–10.9	0.02–0.22	6.8–8.9	0.02–0.07
	Mean	6.8	0.04	7.3	0.08	7.7	0.05
	N	26	18	9	6	11	8
7	Range	4.7–7.5	0.01–0.05	6.1–7.2		6.4–8.1	0.03–0.05
	Mean	6.2	0.02	6.7		7.2	0.04
	N	24	12	7		10	5

[a] Where the largest in a series of developing follicles from laying females (which would have ovulated within 24 hours) = Day 1, the next largest = Day 2, etc.

iteration estimated CORRDAY and follicle diameter at the onset of RFG. I calculated 95% confidence limits around the CORRDAY estimate (Sokal and Rohlf 1981:498).

Polynomial models of RFG (i.e., for data with CORRDAY less than the estimate of beginning of RFG) and postovulatory follicle regression were created to describe relationships between follicle sizes and CORRDAY, with CORRDAY up to the third order. Higher-order variables were removed if nonsignificant ($P > 0.01$). Polynomial models also were derived with CORRDAY as the dependent variable, so that CORRDAY could be predicted from follicles of collected birds.

RESULTS

CORRDAY (and 95% confidence limits) at the beginning of RFG (i.e., duration of RFG) were estimated to be 4.2 (3.8–4.6), 5.1 (4.7–5.6), and 5.0 (4.5–5.4) days for pintails, wigeon, and scaup, respectively; follicle diameters were estimated as 8.2, 6.9, and 7.9 mm, respectively.

Follicle diameters were linearly related to CORRDAY during RFG for all species (Fig. 1). Model intercepts estimated diameters at ovulation as 32.9, 33.8, and 37.1 mm for pintails, wigeon, and scaup, respectively.

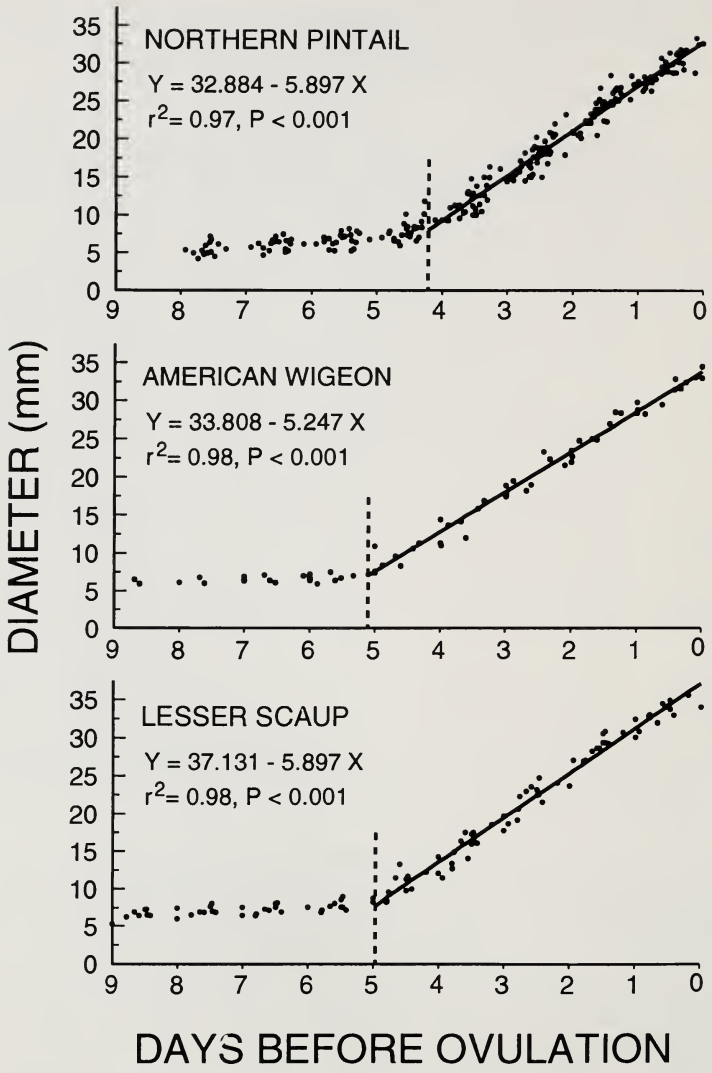

FIG. 1. Rapid follicle growth of three duck species based on ovarian follicle diameters. Vertical dashed lines represent estimates of beginning of rapid follicle growth.

Growth curves of follicle dry masses were best fit with second-order polynomial expressions (Fig. 2). Follicle dry masses at ovulation were estimated to be 8.2, 8.3, and 11.0 g for pintails, wigeon, and scaup, respectively. Predictive models of RFG (Table 2) estimated CORRDAY

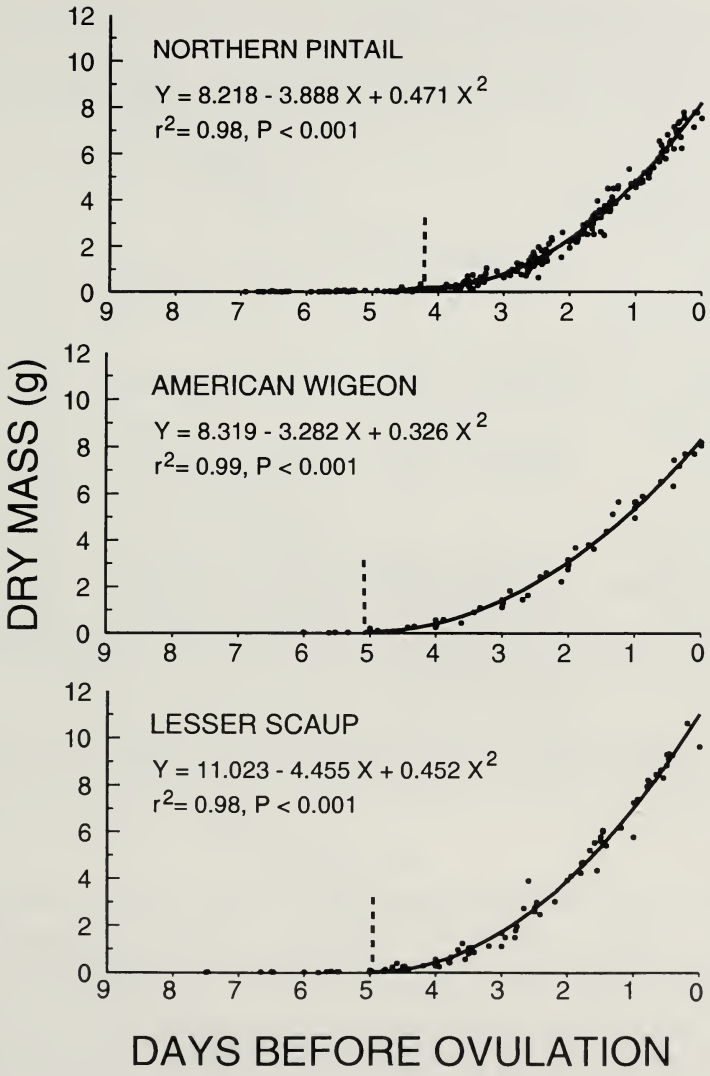

FIG. 2. Rapid follicle growth of three duck species based on ovarian follicle dry masses. Vertical dashed lines represent estimates of beginning of rapid follicle growth.

with linear models of diameter and third-order polynomials of dry mass for all species.

Postovulatory follicle regression was described by second-order polynomials for all species (Fig. 3). Intercepts of these models estimated postovulatory follicle diameter immediately after ovulation as 15.8 mm for

TABLE 2

PREDICTIVE MODELS[a] ESTIMATING CORRDAY[b] FROM OVARIAN FOLLICLE DIAMETERS (DIA) AND DRY MASSES (DRY)

Group	Equation
Rapidly growing follicles	
Northern Pintail	
Diameter	$CORRDAY = 5.451 - 0.164DIA$
Dry mass	$CORRDAY = 3.894 - 1.162DRY + 0.168DRY^2 - 0.011DRY^3$
American Wigeon	
Diameter	$CORRDAY = 6.377 - 0.187DIA$
Dry mass	$CORRDAY = 4.800 - 1.607DRY + 0.263DRY^2 - 0.017DRY^3$
Lesser Scaup	
Diameter	$CORRDAY = 6.217 - 0.166DIA$
Dry mass	$CORRDAY = 4.524 - 1.088DRY + 0.134DRY^2 - 0.007DRY^3$
Postovulatory follicles	
Northern Pintail	$CORRDAY = 6.443 - 0.748DIA + 0.023DIA^2$
American Wigeon	$CORRDAY = 8.714 - 1.105DIA + 0.038DIA^2$
Lesser Scaup	$CORRDAY = 7.744 - 0.823DIA + 0.023DIA^2$

[a] All models $r^2 > 0.96$, $P < 0.001$ for rapidly growing follicles, $r^2 > 0.87$, $P < 0.001$ for postovulatory follicles.
[b] The number of days until ovulation for rapidly growing follicles and days since ovulation for postovulatory follicles.

both pintails and wigeon, and 18.2 mm for scaup. Predictive models (Table 2) can be used to estimate CORRDAY based on diameters of postovulatory follicles.

DISCUSSION

Consistent and objective criteria have not been used for defining beginning of RFG for ducks (i.e., defining a measure for distinguishing between developing and nondeveloping follicles), which is essential for determining breeding status. Ovary masses of 3.0 g have been used for pintails (Krapu 1974), Mallards (*Anas platyrhynchos*; Krapu 1981), and Ring-necked Ducks (*Aythya collaris*; Hohman 1986). Follicle diameters have been used for Ruddy Ducks (*Oxyura jamaicensis*; 8.0 mm; Tome 1984), Canvasbacks (*A. valisineria*; 7.5 mm; Barzen and Serie 1990), and pintails (6.0 mm; Phillips and van Tienhoven 1962, Mann and Sedinger 1993). Follicle dry mass of 0.10 g was used for Northern Shovelers (*Anas clypeata*; Ankney and Afton 1988) and Ring-necked Ducks (Alisauskas et al. 1990). Conservative estimates were obtained by using dry mass of the second smallest "developing" follicle from samples of hens with complete sets of follicles; criteria by this method have included 0.20 g for scaup (Afton and Ankney 1991), 0.40 g for Gadwall (*A. strepera*;

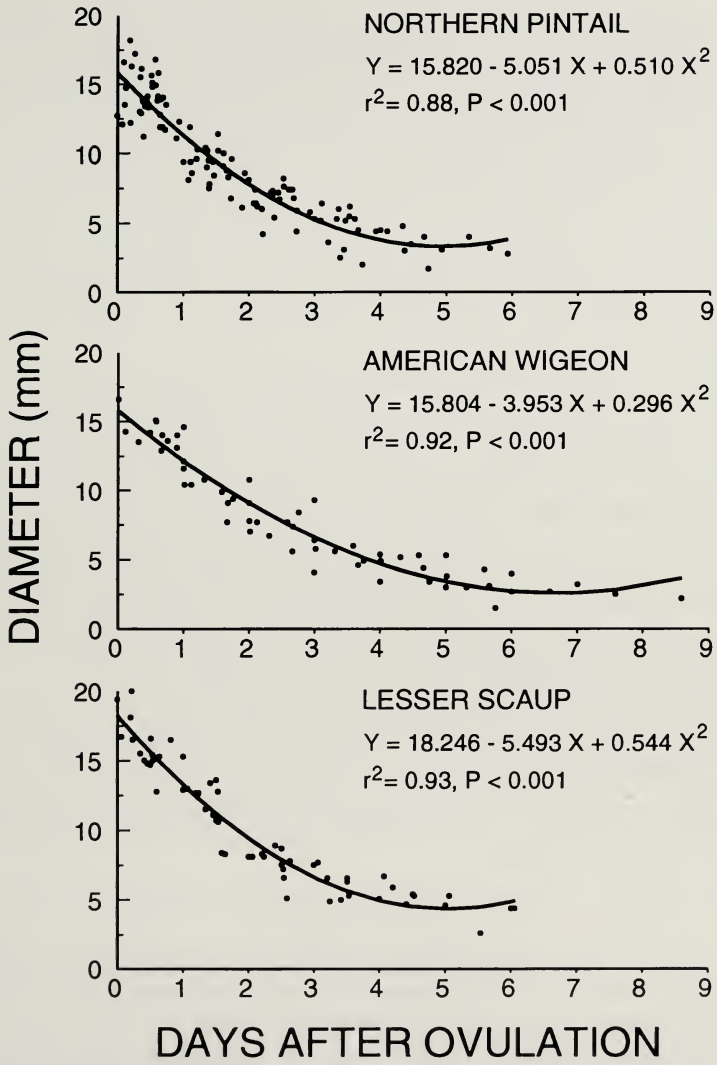

FIG. 3. Regression of postovulatory follicles of three duck species.

Ankney and Alisauskas 1991), and 0.39 g for Mallards (Young 1993). Clearly, it would be valuable to derive consistent methods for interpretation of breeding status from ovaries. Otherwise, there is danger of misinterpreting breeding status and affecting associated analyses.

Initiation of RFG can be determined objectively by the methods presented here. To apply this information to determine waterfowl breeding

status, I suggest adding a conservative buffer to follicle size estimates at the beginning of RFG to be certain that follicles are in RFG. For example, for the species in this study, 10 mm is an appropriate distinction between RFG and non-RFG follicles. Only three pintail follicles were >10 mm before the beginning of RFG (Fig. 1). From polynomial models describing relationships between follicle diameters and dry masses ($P < 0.001$, $r^2 > 0.98$), I found that 10 mm corresponded to 0.12, 0.15, and 0.10 g dry mass for pintails, wigeon, and scaup, respectively; thus, 0.15 g dry mass also is an appropriate distinction for these species. Follicles before the beginning of RFG were <0.15 g, again with the exception of the three pintail follicles.

Duration of RFG can be estimated in several ways. Rough estimates can be obtained by multiplying the maximum number of developing follicles by the egg-laying interval (Alisauskas and Ankney 1992). Renest intervals have been used as a maximum estimate (Grau 1984). Duration of RFG also has been estimated by examining rings in cross-sections of yolk that form as yolk material is deposited; each pair of rings was presumed to represent daily growth (e.g., Grau 1976, 1984; Roudybush et al. 1979; Astheimer and Grau 1990). However, Alisauskas and Ankney (1994) suggested that the ring method may not work for laying waterfowl with a diphasic feeding regime that may lay down more than one set of rings each day. This pattern was found in Japanese Quail (*Coturnix coturnix*) fed twice daily (Dobbs et al. 1976). The method I presented here has advantages over other methods because the results are more exact and, unlike the ring method, laboratory analyses are not required and assumptions regarding yolk deposition are not necessary. However, collection of birds is required.

My estimates of duration of RFG are shorter than the six days previously described for these species (Phillips and van Tienhoven 1962, Alisauskas and Ankney 1992). These results are corroborated by examining ranges and means of follicle sizes by DAY (Table 1) for each species; follicles were nondeveloped, on average, on DAY 5 (4–5 days from ovulation) for pintails and DAY 6 (5–6 days from ovulation) for wigeon and scaup. Without comparably treated data from mid-continent breeding areas, it is unknown if there is geographic variability in RFG duration. Short RFG duration may be advantageous for species that exploit unpredictable food resources or that experience high rates of nest predation (Alisauskas and Ankney 1992). However, shorter RFG results in increased daily costs of egg production (Alisauskas and Ankney 1992, 1994).

Although researchers have used ovary characteristics to determine waterfowl breeding status, other values of RFG models have not been exploited. When applied to ovaries of individuals, these models can identify

important aspects of their basic breeding biology. For example, nest initiation dates of birds with developing follicles can be estimated accurately by determining CORRDAY and adding a day for the time the follicle is in the oviduct (Alisauskas and Ankney 1992). Time of day of ovulation also can be estimated. Models of RFG allow detection of breaks in the follicle hierarchy of individuals late in their laying sequence, differentiating follicles that would be laid from those that would not; in such cases, clutch size is the number of developing follicles plus the number of postovulatory follicles. Some analyses of nutrient reserves require accurate distinction of the number of follicles remaining to be laid (e.g., Ankney and Alisauskas 1991, Esler and Grand 1994). Renesting intervals can be determined by estimating days since ovulation of the last follicle of the first nest (using postovulatory follicle models) and days until laying of the first egg of the renest (using models of RFG). Furthermore, for assessments of nutrient and energy commitment to clutch formation (e.g., Drobney 1980, Astheimer 1986, Alisauskas and Ankney 1994), RFG models could provide accurate daily changes.

Postovulatory follicles have been used as objective measures of clutch size and incidence of brood parasitism (e.g., Kennedy et al. 1989). Persistence of postovulatory follicles is variable among taxa (see review in Semel and Sherman 1991). Postovulatory follicles of Wood Ducks (*Aix sponsa*) were detectable for <30 days after ovulation (Semel and Sherman 1991); I suspect this is true for species in this study also. Models for pintails, wigeon, and scaup described regression of postovulatory follicles for only a few days after ovulation; these have value for determining clutch size and, for birds early in incubation, how long they have been incubating.

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EFFECTS OF SURFACE TEXTURE AND SHAPE ON GRIT SELECTION BY HOUSE SPARROWS AND NORTHERN BOBWHITE

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ABSTRACT.—We evaluated the influence of surface texture and shape on grit selection by House Sparrows (*Passer domesticus*) and Northern Bobwhite (*Colinus virginianus*). Captive birds were given a mixture of two grit types (angular/oblong and rounded/spherical) for seven or 14 days. At the end of this period, most birds (24 of 30 House Sparrows and 21 of 26 Northern Bobwhite) had more angular/oblong and less rounded/spherical grit ($P < 0.01$) in their gizzards than predicted on the basis of availability. An improved understanding of avian responses to surface texture, shape, and other grit characteristics may be useful in reformulating granular pesticides to reduce their attractiveness to birds. *Received 20 Jan. 1994, accepted 4 April 1994.*

Granular pesticides are used extensively for insect control and many are acutely toxic to birds (e.g., Balcomb et al. 1984, Hill and Camardese 1984). One potential route of avian exposure to granular pesticides involves birds' intentional consumption of granules as a source of grit. A better understanding of factors influencing grit preferences may suggest ways to alter granular formulations to reduce their attractiveness to birds and lower the probability that granules will be consumed by birds.

Few data are available on the process of grit selection by birds (e.g., Sadler 1961). Grit choice is probably influenced by physical characteristics of grit particles such as size, color, surface texture, and shape. We evaluated the influence of surface texture and shape on grit selection by House Sparrows (*Passer domesticus*) and Northern Bobwhite (*Colinus virginianus*). These species were chosen for experiments because they are ground-foraging granivores and omnivores, respectively (De Graaf et al. 1985), and thus they represent the feeding guilds of birds most likely to be exposed to granular pesticides. The House Sparrow also was chosen because it uses a large amount of grit compared with other birds (Keil 1973; Gionfriddo and Best, in press).

METHODS

Free-ranging House Sparrows were captured with mist nets at several rural sites in Story County, Iowa. They were fitted with numbered leg bands, transferred to an outdoor aviary, and given at least eight days to acclimate to captivity. Gizzards of House Sparrows then were voided by saline flushing. Each bird was anesthetized by injecting the pectoral muscle with 0.15 cc of ketamine hydrochloride (Vetalar, diluted to 10 mg/ml) to which about 0.005

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FIG. 1. Angular/oblong and rounded/spherical grit used in experiments with House Sparrows (left) and Northern Bobwhite (right).

cc of diazepam (Valium, 5 mg/ml) had been added. We then flushed the gizzard with 30 cc of saline solution (0.9% sodium chloride irrigation, USP) delivered in 20 1.5-cc injections. We used a 10-ml Cornwall syringe pipet with a ball-tipped, straight intubation needle (18 gauge, 7.6 cm long). The needle was long enough to reach a House Sparrow's gizzard when inserted through the mouth. Gizzard contents were hydraulically flushed through the esophagus and mouth while the bird was held in a vertical position, tail up and beak down. This procedure effectively removes all or nearly all food and grit from the gizzards of most House Sparrows, and the recovery rate of the birds is high (92%) (Gionfriddo et al., in press). After recovery from anesthesia, 30 birds were placed in an aviary compartment with food and water. The experiment began when grit was added at dawn the next day.

Juvenile (11-week-old) Northern Bobwhite purchased from a commercial game bird producer were transferred to aviaries where they were held for 18 weeks before being used in the experiment. There was no need to void gizzards of the Northern Bobwhite because grit had been withheld from these birds since hatching.

During acclimation and experiments, House Sparrows and Northern Bobwhite were housed in outdoor aviary compartments measuring 3.7 × 4.6 × 2.1 m and maintained on a commercially prepared wild bird seed mixture (Cardinal Brand Wild Bird Feed, Des Moines Feed Co., Des Moines, Iowa) containing millet, milo, cracked corn, sunflower seeds, peanuts, and wheat. Birds also were provided with vitamin-enriched water. Grit was provided only during experiments.

Two types of grit were used, representing two extremes in surface texture/shape. For House Sparrows, rounded/spherical grit consisted of "blanks" of silica (quartz) granules used for the pesticide FURADAN 15G, and angular/oblong grit was hammermilled "Col-

orado quartz" (Fig. 1). (Best and Gionfriddo [1991] described the system used to characterize grit surface texture/shape; surface textures ranged from well-rounded to angular and shapes from spherical to oblong.) For Northern Bobwhite, clear glass beads were used as rounded/spherical grit and angular/oblong grit was hammermilled clear glass. For both species, the two grit types were identical in mineral composition (quartz or glass), color (clear), and size (both grit types were sieved to a size range of 0.4–0.8 mm for House Sparrows and 1.8–2.4 mm for Northern Bobwhite, respectively; these sizes represent the middle of the normal ranges of grit sizes used by free-ranging birds of these two species [Best and Gionfriddo 1991]). All grit was tumbled in a vibrating tumbler for five days to produce a "frosted" surface similar to that of the silica granules and to dull the jagged edges of the hammermilled grit.

Grit was provided to birds during each experiment in two square grit trays, each measuring 0.5 m^2. Sides of the trays were constructed of 5 × 10 cm lumber, and bottoms consisted of the cement aviary floor. Each tray contained a mixture of equal amounts (by volume) of angular/oblong and rounded/spherical grit. Volumetric measures of grit were used because the large amounts of grit needed in the experiments precluded our counting individual particles provided to birds and necessitated the use of an alternative measure. Each tray was supplied with 10 cc (House Sparrows) or 25 cc (Northern Bobwhite) of grit, which was replaced every two days. Later, we counted the particles in equal volumes of angular/oblong and rounded/spherical grit to determine the proportions of the two grit types in the grit mixtures given to Northern Bobwhite and House Sparrows. Ratios of angular/oblong to rounded/spherical grit were 53:47 for Northern Bobwhite and 35:65 for House Sparrows. These ratios were then used in deriving expected values for Chi-square analysis.

In the House Sparrow experiment, all (30) birds were sacrificed after 14 days; in the Northern Bobwhite experiment, half of the 26 birds were sacrificed after seven days and half after 14 days. Gizzards were removed and preserved in 95% ethanol. Later, each gizzard was sliced in half with a razor blade, and the contents were flushed into a Petri dish and examined carefully under a zoom, stereo microscope. Grit particles were separated from other gizzard contents. Gizzard contents were searched thoroughly at least two times. Grit particles of the two types were then sorted and counted.

RESULTS

All House Sparrows readily consumed the grit provided. The mean grit count per bird was 139.5 (±82.5 [SD]), well within the range of values for free-ranging House Sparrows (Gionfriddo and Best, in press). Twenty-four of 30 birds had greater proportions of angular/oblong grit in their gizzards than if they had consumed grit randomly (Chi-square analysis, $P < 0.01$); three had significantly more rounded/spherical grit (Fig. 2). Only three birds had no apparent grit surface texture/shape preference. Ratios of angular/oblong to rounded/spherical particles in their gizzards did not differ from 35:65.

Gizzard contents of Northern Bobwhite given grit for seven days were similar to those of 14-day birds. All birds in both groups consumed grit, and mean grit counts per bird did not differ between groups ($t = 0.12$, df = 23, $P = 0.91$; 7-day birds: $\bar{x} = 145.5 \pm 81.6$, 14-day birds: $\bar{x} = 148.9 \pm 68.8$). Furthermore, the proportion of the grit particles that were angular/oblong did not differ between gizzards of the two groups of birds

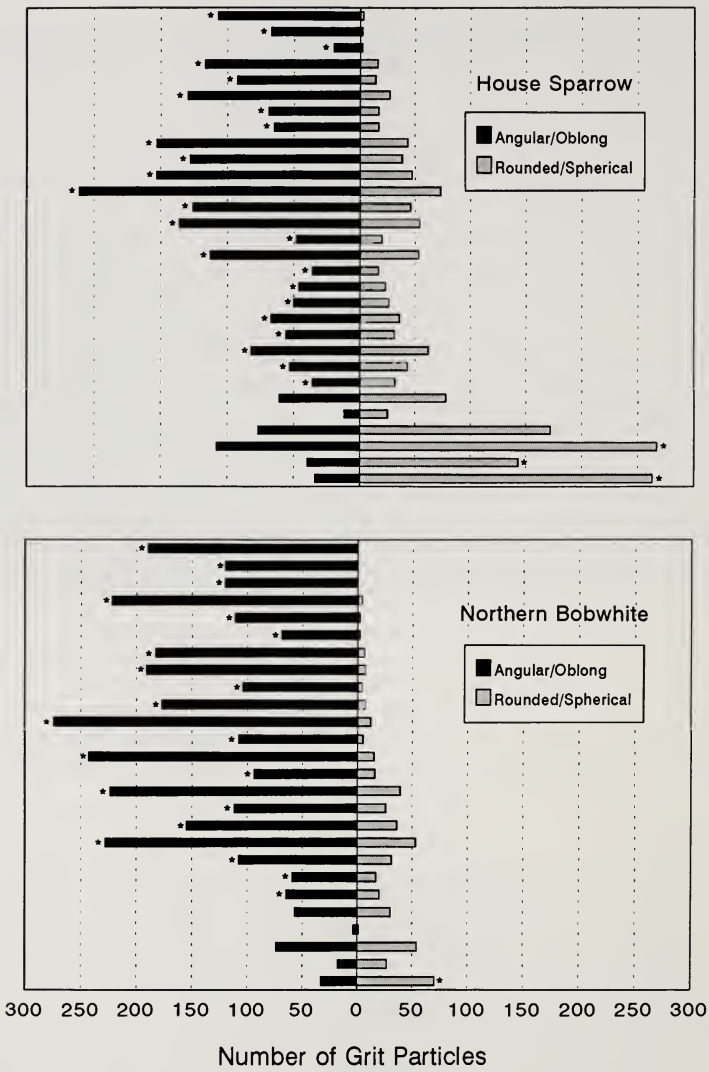

FIG. 2. Angular/oblong and rounded/spherical grit particles in gizzards of House Sparrows and Northern Bobwhite given a mixture of the two types of particles. Asterisks denote birds that consumed one grit particle type in proportions greater than expected on the basis of its availability (Chi-square analysis, $P < 0.01$).

($t = 1.68$, df = 19, $P = 0.11$). Consequently, the 7-day and 14-day data sets were combined. Twenty-one of 26 gizzards contained greater proportions of angular/oblong than rounded/spherical grit, and one gizzard contained more rounded/spherical grit (Chi-square analysis, $P < 0.01$). Proportions of the two grit types in the remaining four gizzards did not differ significantly.

DISCUSSION

House Sparrows and Northern Bobwhite used in our experiments differed in several ways. The House Sparrows formerly were free-ranging birds experienced in using grit, whereas the Northern Bobwhite were captive-raised juveniles never exposed to grit. The two species also are very different in body size and represent different avian orders. Despite these differences, the responses of House Sparrows and Northern Bobwhite were very similar in our experiments. Both species clearly expressed a preference for angular/oblong rather than rounded/spherical grit when given a mixture of the two types. The occurrence of this preference in birds with prior experience in grit use and in birds with no prior exposure to grit suggests the preference may have a genetic basis.

Grit preferences may be related to diet. The amounts, sizes, and shapes of grit used by birds vary with diet (e.g., Norris et al. 1975, Alonso 1985, Norman and Brown 1985, Hogstad 1988). Perhaps certain grit surface textures/shapes increase the efficiency of digestion of some foods more effectively than others. Based on examination of grit, Smith and Rastall (1911) suggested that Red Grouse (*Lagopus l. scoticus*) needed "subangular and roughly rounded" small pebbles to grind foliage of *Calluna* and that grit with cutting edges and sharp points was unsuitable. The House Sparrows and Northern Bobwhite may have selected angular/oblong grit because it more efficiently ground the seeds they ate. The degree to which diet influences grit selection has not been tested formally.

Grit present in a bird's gizzard depends not only upon selection of particles for consumption, but also upon the dynamics of retention in the gizzard. Grit selection, as we have measured it here, thus includes a component of grit retention. Particle characteristics such as surface texture and shape may influence retention of grit. We conducted other experiments with captive House Sparrows to evaluate the relative contribution of grit-retention processes to the surface texture/shape of grit present in gizzards (Best and Gionfriddo, unpubl. data). Birds were administered (oral gavage) or fed (mixed with canned dog food) equal amounts of the angular/oblong and rounded/spherical grit for a period of time, deprived of grit for two days, and then sacrificed. In both experiments, the proportions of the two grit types did not differ (Chi-square analysis, $P >$

0.5) in most gizzards. The results of these retention experiments suggest that surface texture/shape may not influence grit retention. We conclude that the grit-use patterns observed in gizzards of experimental House Sparrows and Northern Bobwhite reflect differential selection (rather than differential retention) of angular/oblong and rounded/spherical particles.

Although grit selection may be the primary factor determining the grit in birds' gizzards, it can be constrained by availability of grit of various types. Grit selection also may be affected by diet, characteristics of grit already in the gizzard, and other factors. More experimental work is needed, with additional avian species, before we will have a clear understanding of avian grit preferences and of the influences of grit characteristics such as surface texture/shape on grit choice and retention in birds. Such knowledge may be useful in "designing" granular pesticides to make them less attractive to birds.

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22nd INTERNATIONAL ORNITHOLOGICAL CONGRESS

The 22nd International Ornithological Congress will be held in Durban, South Africa from 16–22 August 1998. Professor Peter Berthold (Germany) will serve as President, Dr. Janet Kear (United Kingdom) as Vice President and Dr. Aldo Berruti as Secretary-General. This Congress will include a full scientific program and a large series of ornithological tours to numerous areas within southern Africa. All interested ornithologists are invited to take part.

Potential members of the Durban congress are requested to contact Dr. Aldo Berruti (Durban Natural Science Museum, PO Box 4085, Durban 4000, South Africa) to be placed on the mailing list, or to provide suggestions on any aspects of the 22nd congress. Persons on the mailing list will be sent information on all aspects of the congress in proper time.

The chairman of the Scientific Program Committee is Dr. Lukas Jenni (Schweizerische Voegelwarte, CH-6204 Sempach, Switzerland). Suggestions for the scientific program should be sent to him. Announcements for the scientific program will be published separately. Letters of inquiry about the scientific program can be sent to Dr. Lukas Jenni, Professor Peter Berthold, Professor Walter Bock (Secretary of the IOC, Box 37 Schermerhorn Hall, Dept. of Biological Scienes, Columbia Univ., New York, New York 10027, USA).

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EXTENDED FLIGHT-SONGS OF VESPER SPARROWS

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ABSTRACT.—While conducting fieldwork on the breeding ecology of grassland birds at Kennebunk, Maine, we documented the existence of extended flight-songs of Vesper Sparrows (*Pooecetes gramineus*). In general, we observed this behavior very infrequently, usually less than three times per breeding season. Extended flight-songs were about three times as long as primary songs and contained elements not typically found in primary songs. Extended flight-songs occurred more frequently late in the breeding season. Within the subfamily Emberizinae, extended flight-songs have now been documented for at least 10 species but their behavioral function remains unclear. *Received 8 Nov. 1993, accepted 21 April 1994.*

In a recent review, Spector (1992) classified the song systems of wood-warblers (Parulinae) into subsets. For some genera, he distinguished between "primary" song—a song type used most frequently and often given less frequently after mating—and "extended" song—a song type heard less commonly and often given in flight. Extended songs are best known from the Parulinae (Ficken and Ficken 1962, Spector 1992), most notably Common Yellowthroat (*Geothlypis trichas*) (Ritchison 1991) and Ovenbird (*Seiurus aurocapillus*) (Lein 1981). At least 17 species of Emberizinae also have extended songs, and in at least ten species these songs are typically given in flight (Table 1). Within the Emberizinae, only Cassin's Sparrow (*Aimophila cassinii*), Lark Bunting (*Calamospiza melanocorys*), *Calcarius* longspurs, and *Plectrophenax* buntings regularly sing their primary song in flight (Austin 1968a).

METHODS AND RESULTS

During the course of fieldwork on the breeding ecology of grassland birds in Kennebunk, Maine (43°23′N, 70°37′W), we documented the "extended flight-song" of Vesper Sparrows (*Pooecetes gramineus*). The infrequency of this behavior may explain why it has not been well-documented; it also complicates interpretation of its function. Until July 1993, we had observed this behavior among a population of 50–100 pairs only 24 times during eight of 10 field seasons, despite being in the field for >40 h/week for the entire breeding season. The exception came on the mornings of 28 and 30 July 1993 when Wells noted at least 20 extended flight-songs and recorded several examples (Cornell Laboratory of Ornithology, Library of Natural Sounds Catalog Numbers 55508–55511 and 63000). During this observation period there was an average of one extended flight-song every 15–20 min in an area where 8–10 pairs of Vesper Sparrows had established territories.

Extended songs of Vesper Sparrows differ in several ways from their primary songs (Figs. 1 and 2). They are longer, approximately 6–10 sec in duration compared to primary song

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TABLE 1

SPECIES OF EMBERIZINAE FOR WHICH EXTENDED SONGS HAVE BEEN DOCUMENTED

Species	Song characteristics	Reference
California Towhee (*Pipilo crissalis*)	P, U, I	Childs 1968
Bachman's Sparrow (*Aimophila aestivalis*)	F, U, I	Mengel 1951
Field Sparrow (*Spizella pusilla*)	P	Nelson and Croner 1991
Vesper Sparrow (*Pooecetes gramineus*)	F, U, I	Present study, Burroughs 1905
Lark Sparrow (*Chondestes grammacus*)	F, C	Baepler 1968
Grasshopper Sparrow (*Ammodramus savannarum*)	P	Smith 1959
Henslow's Sparrow (*A. henslowi*)	F, U, I	Graber 1968
LeConte's Sparrow (*A. leconteii*)	P?, U, I	Walkinshaw 1968
Sharp-tailed Sparrow (*A. caudacutus*)	F, U	Greenlaw 1993
Seaside Sparrow (*A. maritimus*)	F, U	McDonald 1983
Song Sparrow (*Melospiza melodia*)	F, U, I	Nice 1943
Lincoln's Sparrow (*M. lincolnii*)	F, U, I	Speirs and Speirs 1968
Swamp Sparrow (*M. georgiana*)	F, U, I	Wetherbee 1968, Nowicki et al. 1991
Rufous-collared Sparrow (*Zonotrichia capensis*)	N, U	Lougheed and Handford 1989
Harris' Sparrow (*Z. querula*)	P, U, I	Baumgartner 1968
Dark-eyed Junco (*Junco hyemalis*)	P, U, I	Eaton 1968
Yellow-eyed Junco (*J. phaeonotus*)	F, C, I	Austin 1968b

F = extended song typically given in flight; P = extended song typically given from a perch; C = extended song included in courtship display; U = behavioral context of extended song unclear; I = extended song normally occurs infrequently; N = extended song given at night.

length of 2.4–4.2 sec (Berger 1968). Like extended songs of many species, the extended songs of Vesper Sparrows begin with several "chip" notes then continue with a series of trills at various frequencies and speeds bearing little resemblance to primary songs (Fig. 2).

In most cases, no other Vesper Sparrows were singing when this behavior occurred. During 322 min of observation on 28 and 30 July, the only primary songs heard were delivered by one bird that sang eight times over a 5-min period. On 30 July a recording of the primary song of a Vesper Sparrow that elicited strong response early in the season was played near areas where extended flight-songs had been recently noted. This did not elicit flight songs or any other obvious response. We think that these extended flight-songs were delivered by resident males, most of whom had been on territory since early May; no agonistic territorial behavior was ever observed subsequent to an extended flight-song.

In a typical extended flight-song, the singing Vesper Sparrow ascended to a height of 25–75 m and moved horizontally and in a straight line 100–200 m before descending. Flight-songs were noted throughout the day and often (>50%) occurred under cloudy, overcast skies. Because of the infrequency and apparent unpredictability of this behavior we had few opportunities to examine closely individuals giving extended songs. On 30 July, however, Wells closely examined a bird that had completed an extended flight-song 50 m from him. The bird was clearly an adult as evidenced by its worn plumage.

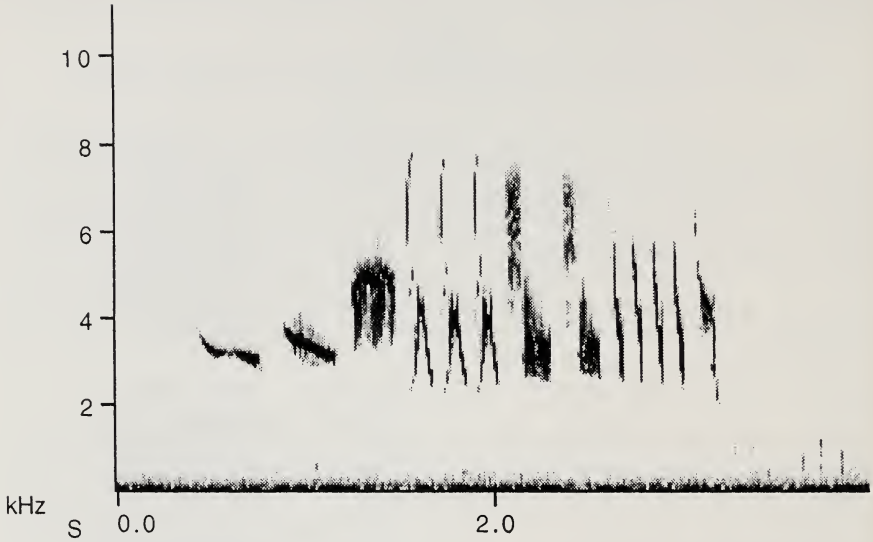

FIG. 1. Sonogram of primary song of a Vesper Sparrow recorded 30 May 1951 near Ithaca, New York (Cornell Laboratory of Ornithology, Library of Natural Sounds Catalog Number 15364). Note that the song lasts approximately three sec. Sonograms were produced using Canary 1.1 software from the Cornell Bioacoustics Research Program.

Extended flight-songs were usually given by Vesper Sparrows late in the breeding season (Fig. 3). Although sparrows arrived at our study site in April and began first nests in May, the earliest date that we noted an extended flight-song was 29 June. All other extended flight-songs occurred between 7 July–10 August. This pattern suggests that the function of Vesper Sparrow extended flight-song is not normally associated with territorial interactions or mate attraction.

DISCUSSION

Ritchison (1991) found that male Common Yellowthroats uttered extended flight-songs more frequently when he was within their territory and proposed that this behavior may function to warn a mate of potential predators and/or to distract the predator away from a nest site. This explanation seems inadequate for Vesper Sparrows at this site because nest predation rates averaged 58% between 1984–1986 (Vickery et al. 1992). If the extended flight-songs of Vesper Sparrows function as a predator warning to mates, one would expect this behavior to occur more frequently and earlier in the season. Other possible explanations include the possibility that extended flight-songs may function as a predator warning to fledglings or may function to bring fledglings together by broadcasting

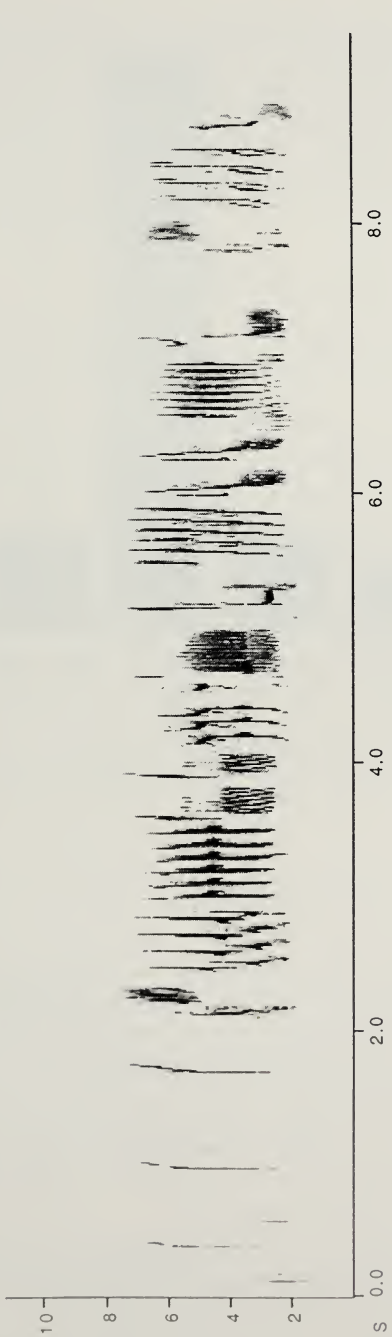

FIG. 2. Sonogram of an extended flight-song of a Vesper Sparrow recorded 30 July 1993 at Kennebunk, Maine (Cornell Laboratory of Ornithology, Library of Natural Sounds Catalog Number 63000). Note that the song lasts approximately nine sec and is different in structure from the primary song in Fig. 1.

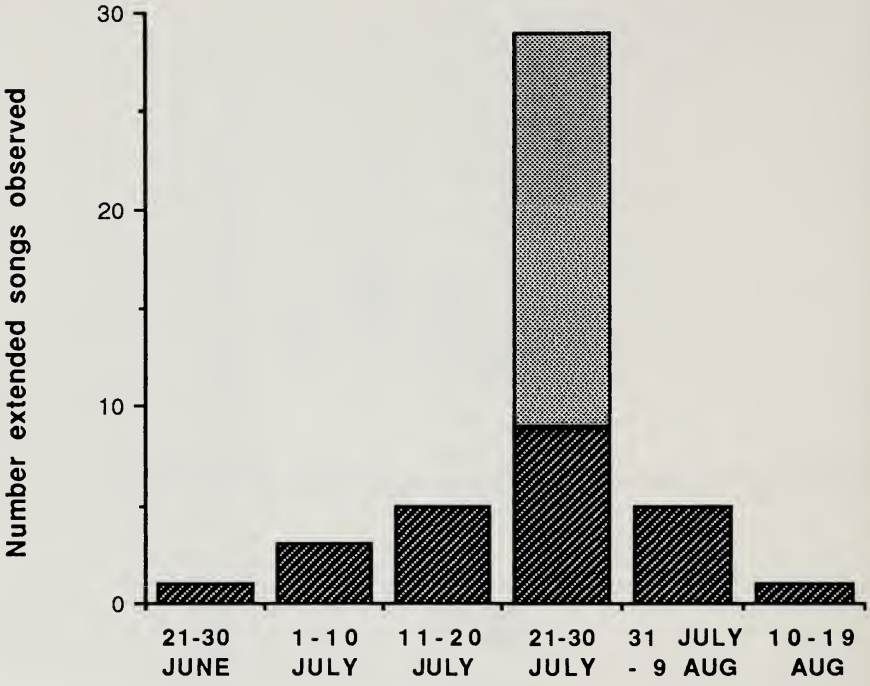

FIG. 3. Number of Vesper Sparrow extended flight songs noted in six ten-day periods from June through August 1984–1993 at Kennebunk, Maine. Observer effort was approximately equal among time periods. Stippled bar represents 1993 observations described in text.

a long, distinctive song from a height that would increase the area of audibility.

The use of extended flight-songs suggests a phylogenetic link between those Paruline warblers with an extended song (*Protonotaria, Helmitheros, Limnothlypis, Seiurus, Oporornis,* and *Geothlypis* [Spector 1992]) and the Emberizines. It is unclear, however, whether or not extended song is homologous in the two groups or whether it could have evolved independently in each. Even if extended flight-song in both groups has a common origin, it may not serve the same function for all species.

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PATTERNS OF STOPOVER BY WARBLERS DURING SPRING AND FALL MIGRATION ON APPLEDORE ISLAND, MAINE

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Abstract.—Migrant warblers mist netted on Appledore Island, Maine, during spring and fall migration in 1990 and 1991 allowed analysis of seasonal differences in stopover patterns, including recapture rates, stopover lengths, and changes in mass and fat during stopover. Northern Waterthrushes (*Seiurus noveboracensis*) and American Redstarts (*Setophaga ruticilla*) had higher recapture rates in the fall than in the spring on Appledore Island. The Ovenbird (*Seiurus aurocapillus*) and the Canada Warbler (*Wilsonia canadensis*) had significantly longer stopovers in the fall than in the spring. During fall migration, young Northern Waterthrushes were more likely to be recaptured than adults, and young American Redstarts had longer stopovers than adults. During spring migration, female Magnolia Warblers (*Dendroica magnolia*) were more likely to be recaptured than males. Higher numbers of both male and female American Redstarts were recaptured in the fall than in the spring. American Redstarts, Northern Waterthrushes, and Ovenbirds showed no significant increase in fat class in the spring, while exhibiting significant increases in fat class in the fall. These three species also exhibited significant increases in mass during fall migration, while only the Ovenbird significantly increased mass in the spring. These data suggest that migrants show species, age, and sex specific seasonal differences in stopover pattern as well as differences in mass and fat accumulation. Such differences are likely affected by hormone titer, risk of predation, seasonal/temporal changes in weather patterns, and/or differences in food availability. Moreover, stopover sites may be used differently as a result of seasonal differences in relation to ecological barriers as well as distances to either breeding or wintering grounds. *Received 28 April 1993, accepted 20 April 1994.*

Few researchers have investigated differences in the stopover biology of migratory passerines between spring and fall migration (e.g., Rappole and Warner 1976; Cherry 1982; Safriel and Lavee 1988; Winker et al. 1992a, b, c; Weisbrod et al. 1993), and none of these studies was conducted along the western North Atlantic Ocean. Moreover, studies comparing age and sex differences in the stopover biology within species are few in number (e.g., Ellegren 1991, Lavee et al. 1991). Because patterns of passerine migration differ between seasons (Rappole and Warner 1976, Yom-Tov 1984) and timing of migration differs between age and sex groups (Francis and Cooke 1986, Ellegren 1991), patterns of stopover behavior may also differ among these groups and seasons.

In the spring, migrants presumably must arrive at breeding sites early to establish quality territories, but not so early as to risk mortality, from

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inclement weather, predation, or inadequate food supply (Francis and Cooke 1986). Fall migrants must leave in time to find adequate food supplies and favorable weather for their migration, and are faced with competition both enroute to and on their wintering grounds. Spring migrants face the same pressures but have the added requirement of returning early enough to secure productive breeding territories. This would be particularly true of males (Francis and Cooke 1986) and for this reason we expect shorter stopovers and fewer recaptures of migrants, especially males, in spring than in fall. Also one might predict that lean birds should remain longer at stopover sites than those with sufficient energy reserves. This prediction particularly is logical for spring migrants who are close to their final destination.

In this study we attempted to answer the following questions (1) Do migrant species exhibit different patterns of stopover during spring and fall migration? (2) Do age and sex classes have different patterns of stopover between seasons? (3) Are the fat classes of migrants arriving on Appledore Island different between seasons? and (4) Do migrants experience similar changes in fat class and mass during stopover between seasons?

STUDY SITE AND METHODS

We mist netted warblers on Appledore Island, Maine (42°58′N 70°36′W), a 33.6-ha island in the Gulf of Maine (Fig. 1). Appledore is the largest island in the Isles of Shoals, a group of nine small islands and several ledges 14.5 km southeast of Portsmouth, New Hampshire, and 9.7 km from the nearest point of the mainland. While most of the islands are sparsely vegetated with much of their area composed of exposed rock, Appledore has a variety of vegetation types. Lyman (1988) estimates that one-third of Appledore's area is exposed rock, with the remaining two-thirds divided into vegetation of four types (1) upland meadow and low shrubs, characterized by grasses, forbs, rose (*Rosa virginiana*), poison ivy (*Rhus radicans*), goldenrod (*Solidago* sp.), choke cherry (*Prunus virginiana*), and raspberry (*Rubus* sp.); (2) interior low-lying areas of high shrubs including winterberry (*Ilex verticillata*), apple (*Pyrus* sp.), and pin cherry (*Prunus pensylvanicus*); (3) disturbed areas covered mainly with grasses, forbs, sumac (*Rhus typhina*), and poplar (*Populus* sp.); and (4) wetland areas characterized by cattails (*Typha latifolia*), rushes (*Scirpus* sp. and *Juncus* sp.), iris (*Iris versicolor*), grasses and smartweed (*Polygonum* sp.). Upland meadows and low shrubs and interior areas of high shrubs comprise approximately 37% and 45% of the vegetated areas of the island, respectively (Lyman 1988). Appledore is the only island in the Isles of Shoals with available fresh water.

We captured birds between 18 May and 8 June in 1990, 15 May–6 June in 1991 (3545 total net-h), 16 August–20 September in 1990, and 16 August–21 September in 1991 (5877.5 total net-h). Weather permitting, we operated six to ten mist nets (12 × 2.6 m, 30 mm mesh) during most of the daylight hours, with the mist nets opened just before sunrise, closed around sunset, and checked approximately every 30 min throughout the day. We banded birds with U.S. Fish and Wildlife Service bands as they were brought to a central location. For each bird captured (and recaptured), we recorded age and sex, the degree of skull pneumatization, unflattened wing chord (0.5 mm), fat class (see below), and mass (0.01 g).

FIG. 1. Map of the New England coast showing the location of the Isles of Shoals (courtesy of the Shoals Marine Laboratory).

In the case of recaptures, we did not refer to the initial data sheets, so that measurements were not influenced by information previously recorded. The fat classification system we use is similar to that described by Cherry (1982). Because only a few individuals were assigned fat classes of 3 or 4 each season (3.9% overall, N = 2770), we included birds with a fat class of 3 or 4 with the individuals in fat class 2 in our analysis.

We calculated minimum length of stopover by subtracting the initial date of capture from the date of last recapture (Cherry 1982, Moore and Kerlinger 1987, Ellegren 1991). Thus, a one-day stopover refers to a stopover of one night and part of two days. This method differentiates between passage migrants, birds that interrupt migration only during the day but presumably continue migration that night, and stopover migrants, birds that suspend migration for at least one night. This method resulted in a conservative estimate of the time a migrant remained at the site because we could not assume that the date of initial capture

was the first day of a stopover nor could we assume that the final recapture occurred on the last day of a stopover (Cherry 1982, Biebach et al. 1986, Moore and Kerlinger 1987). Average stopover lengths would be biased if residents as well as migrants of the same species were included in the analysis. Thus we excluded Common Yellowthroats (*Geothlypis trichas*) and Yellow Warblers (*Dendroica petechia*) from this analysis because they are confirmed regular breeders on Appledore Island (Borror and Holmes 1990).

When comparing mass between initial capture and subsequent recaptures, mass must be taken at the same time of day (Rappole and Warner 1976) or corrected to the same time of day (Cherry 1982, Moore and Kerlinger 1987, Loria and Moore 1990). We corrected mass to 12:00 DST for all individuals by computing the average percent mass gain per hour using individuals captured more than 5 h apart on the same day (Moore and Kerlinger 1987, Loria and Moore 1990). Migrant warblers had an average hourly mass gain of 0.210 ± 0.401% (N = 51 individuals). We computed an individual's mass change by subtracting the initial mass from the final mass.

In many passerine species, males tend to be larger than females, and adults tend to be larger than young birds. Males also often have longer wing chords than do females. To compare increases in mass, we calculated the percent gain during stopover using the following formula: percent gain = (final mass − initial mass)/initial mass × 100%. Daily increases in mass were calculated by dividing the percent gain by stopover length. This method reduces the possibility of sex or age related size differences influencing observed differences in mass.

Significance levels of statistical tests between spring and fall denote one-sided probabilities to reflect our expectation of fewer recaptures and shorter stopovers in the spring. Because we expected increases in fat class and mass during stopover, tests on fat and mass changes were also one-sided. All other statistical tests reflect two-sided probabilities. In the case of two sample *t*-tests, we did not assume equal variance and therefore we present results using degrees of freedom corrected for unequal variance.

RESULTS

During 1990 and 1991, we banded 3412 birds of 69 species during spring migration and 2723 individuals of 82 species during fall migration. We present results here from the 1722 migrant warblers captured during spring migration and the 1048 migrant warblers captured during fall migration (Table 1).

Migrants were more likely to be recaptured in the fall than in the spring. Only the Magnolia Warbler (scientific names in Table 1) had a higher recapture rate in the spring than in the fall, but this particular difference between seasons was not statistically significant (Table 2). Migrant warblers also tended to stop longer during fall migration than during the spring. Although most species tended to have longer stopovers in the fall than in the spring (Table 3), only the Ovenbird and the Canada Warbler differed significantly in this regard (Mann-Whitney *U*-test, $U = 72.5$, $P = 0.016$; and $U = 6.0$, $P = 0.026$, respectively). Within the Parulinae, we found significantly different stopover lengths between species in the fall (Kruskal-Wallis test, $t = 13.97$, $P = 0.03$). However, in the spring,

TABLE 1

CAPTURES BY SEASON (1990–1991) OF WARBLER SPECIES WITH MORE THAN 10 INDIVIDUALS CAPTURED ON APPLEDORE ISLAND, MAINE

	Spring			Fall		
	N	Date range[a]	Median	N	Date range[a]	Median
Blue-winged Warbler (*Vermivora pinus*)	0	—	—	33	228–254	239
Tennessee Warbler (*V. peregrina*)	6	139–144	141	9	234–254	246
Nashville Warbler (*V. ruficapilla*)	7	138–158	145	17	229–260	252
Northern Parula (*Parula americana*)	33	136–152	141	6	252–264	258–9
Chestnut-sided Warbler (*Dendroica pensylvanica*)	34	136–157	145	38	228–261	239
Magnolia Warbler (*D. magnolia*)	578	136–159	146	51	232–264	252
Cape May Warbler (*D. tigrina*)	1	141	—	56	229–263	251
Black-throated Blue Warbler (*D. caerulescens*)	40	136–155	140	21	239–261	250
Black-throated Green Warbler (*D. virens*)	12	136–156	144	8	229-262	251
Blackburnian Warbler (*D. fusca*)	32	136–158	151	5	238–261	254
Prairie Warbler (*D. discolor*)	0	—	—	15	228–256	233
Bay-breasted Warbler (*D. castanea*)	20	139–152	146–7	15	240–263	252
Blackpoll Warbler (*D. striata*)	122	136–159	147	56	228–264	255
Black-and-white Warbler (*Mniotilta varia*)	44	136–153	141	59	228–261	240
American Redstart (*Setophaga ruticilla*)	337	135–159	148	176	228–262	251
Ovenbird (*Seiurus aurocapillus*)	79	136–158	144	51	228–261	243
Northern Waterthrush (*S. noveboracensis*)	70	136–159	144–5	233	228–261	245
Mourning Warbler (*Oporornis philadelphia*)	53	145–159	152	44	228–259	240
Wilson's Warbler (*Wilsonia pusilla*)	33	136–152	140	62	229–260	246
Canada Warbler (*W. canadensis*)	177	137–158	149	47	229–264	239
Yellow-breasted Chat (*Icteria virens*)	0	—	—	26	234–262	248–9

[a] Earliest and latest Julian date of capture.

TABLE 2

COMPARISON OF RECAPTURE RATES DURING SPRING AND FALL MIGRATION ON APPLEDORE ISLAND, MAINE

Species	Spring		Fall		χ^2	*P*
	N	Percent recaptured	N	Percent recaptured		
Magnolia Warbler	676	1.78%	51	0.00%	1.00	0.320
Blackpoll Warbler	122	0.00%	56	3.57%	4.41	0.036
Black-and-white Warbler	44	6.82%	59	15.25%	1.74	0.187
American Redstart	337	3.18%	176	13.64%	21.54	0.001*
Mourning Warbler	53	1.89%	44	9.09%	2.55	0.110
Ovenbird	79	8.86%	51	25.49%	6.58	0.010
Northern Waterthrush	70	2.86%	233	17.60%	9.60	0.002*
Canada Warbler	177	1.69%	47	4.26%	1.12	0.291
Total	1722	2.26%	1048	11.07%	95.59	0.000*

* Significant at $\alpha = 0.05$ after sequential Bonferroni correction for multiple tests.

individual species did not differ significantly in the average length of stopover ($t = 9.28$, $P = 0.10$).

The age ratio of individuals captured between seasons was not significantly different ($\chi^2 = 2.28$, df = 1, $P = 0.131$). During spring migration, young birds (hatch-year individuals in the fall and second-year individuals in the spring) comprised 93.9% of the individuals captured (N = 1271), and in the fall young birds accounted for 92.4% of the individuals captured (N = 1047; Table 4). Young American Redstarts and Ovenbirds

TABLE 3

COMPARISON BETWEEN SEASONS OF THE MEAN MINIMUM LENGTH OF STOPOVER ON APPLEDORE ISLAND, MAINE

Species	Spring			Fall		
	N[a]	Mean[b]	Range[c]	N[a]	Mean[b]	Range[c]
Magnolia Warbler	12	2.6 ± 2.1	1–7	0	—	—
Chestnut-sided Warbler	0	—		4	1.5 ± 1.0	1–3
Black-and-white Warbler	3	5.7 ± 5.0	1–11	9	4.1 ± 5.0	1–17
American Redstart	12	2.6 ± 1.5	1–6	24	3.4 ± 3.8	1–18
Ovenbird	7	2.4 ± 1.0	1–4	13	5.1 ± 2.8	1–13
Northern Waterthrush	2	6.0 ± 0.0	6	41	4.3 ± 3.3	1–16
Canada Warbler	3	1.0 ± 0.0	1	2	3.0 ± 1.4	2–4
Total	39	2.9 ± 2.2	1–11	116	3.9 ± 3.4	1–18

[a] Number of individuals recaptured.
[b] Mean and standard deviation of stopover length in days.
[c] Range of stopover length in days.

TABLE 4

COMPARISON OF PROPORTION OF YOUNG INDIVIDUALS CAPTURED DURING SPRING AND FALL MIGRATION ON APPLEDORE ISLAND, MAINE

Species	Spring		Fall	
	N[a]	Percent young	N[a]	Percent young
Magnolia Warbler	492	95.9%	51	90.2%
Chestnut-sided Warbler	31	93.6%	38	97.4%
Blackpoll Warbler	102	97.1%	56	83.9%
Black-and-white Warbler	36	100.0%	59	96.6%
American Redstart	245	81.6%	176	90.9%
Mourning Warbler	20	100.0%	44	97.7%
Ovenbird	24	100.0%	51	98.0%
Northern Waterthrush	13	100.0%	232	87.1%
Canada Warbler	161	99.4%	47	95.7%
Total	1124	93.7%	754	91.1%

[a] Number of individuals that could be aged (based on age keys in Pyle et al. [1987]).

were more likely to be recaptured in the fall than in the spring (χ^2 = 13.1, df = 1, $P < 0.001$: χ^2 = 3.13, df = 1, P = 0.036, respectively). Young Northern Waterthrushes were more likely to be recaptured than adults during fall migration (χ^2 = 2.87, df = 1, P = 0.045). During fall migration, young American Redstarts had significantly longer stopovers than adults (U = 10.0, P = 0.03).

The sex ratios of individuals captured during spring and fall migration were essentially equal (χ^2 = 0.0, df = 1, P = 0.99). Females accounted for just over 51% of the individuals captured in both seasons (Table 5).

TABLE 5

COMPARISON OF RECAPTURES BY SEX FOR FOUR SPECIES OF WARBLERS DURING SPRING AND FALL MIGRATION ON APPLEDORE ISLAND, MAINE

Species	Females				Males			
	Spring		Fall		Spring		Fall	
	N[a]	Percent recaptured	N[a]	Percent recaptured	N[a]	Percent recaptured	N[a]	Percent Recaptured
Magnolia Warbler	267	3.3%	19	0.0%	300	0.3%	24	0.0%
Black-and-white Warbler	38	7.9%	32	18.8%	7	0.0%	27	11.1%
American Redstart	160	3.8%	79	15.2%	217	2.7%	93	11.8%
Canada Warbler	110	2.7%	29	3.5%	66	0.0%	17	5.9%

[a] Number of individuals recaptured.

TABLE 6
COMPARISON OF FAT CLASS DURING SPRING AND FALL MIGRATION ON APPLEDORE ISLAND, MAINE

Species	Spring		Fall	
	N	Percent lean[a]	N	Percent lean[a]
Magnolia Warbler	578	52.6%	51	84.3%
Chestnut-sided Warbler	38	70.6%	34	52.6%
Blackpoll Warbler	122	11.5%	56	82.1%
Black-and-white Warbler	44	34.1%	59	22.0%
American Redstart	377	62.6%	175	66.9%
Mourning Warbler	53	66.0%	44	45.5%
Ovenbird	79	40.5%	50	30.0%
Northern Waterthrush	68	32.4%	232	22.0%
Canada Warbler	177	84.2%	46	71.7%

[a] Percentage of individuals in fat class 0 or 0.5.

Both female and male American Redstarts were more likely to be recaptured during fall migration than during spring migration (females: $\chi^2 = 9.94$, df = 1, $P \leq 0.001$; males: $\chi^2 = 10.32$, df = 1, $P \leq 0.001$). Female Magnolia Warblers were more likely to be recaptured than males during spring migration ($\chi^2 = 7.22$, df = 1, $P = 0.007$). No differences in proportion of individuals recaptured by sex were detected during fall migration in any species.

Six species were leaner during spring migration than during fall migration and only three species were leaner in the fall (Table 6). Magnolia Warblers captured in the spring were significantly fatter than those captured in the fall ($\chi^2 = 19.06$, df = 1, $P \leq 0.001$). Likewise, Blackpoll Warblers captured during the spring were significantly fatter than those captured during the fall ($\chi^2 = 85.78$, df = 1, $P \leq 0.001$). Small sample sizes did not allow a comparison of initial fat class of individuals captured only once with that of recaptured individuals.

A pattern of no significant change in fat class during the spring and significant increases in fat class in the fall was found in American Redstarts (spring: $Z = 1.155$, $P = 0.124$; fall: $Z = 2.758$, $P = 0.003$), Northern Waterthrushes (spring: $Z = 0.447$, $P = 0.328$; fall: $Z = 2.985$, $P = 0.002$), and Ovenbirds (spring: $Z = 1.414$, $P = 0.079$; fall: $Z = 2.081$, $P = 0.019$; Fig. 2).

Migrants stopping over in the fall gained significantly more mass, as a percentage of initial mass, than migrants stopping in the spring ($t = 2.64$, df = 77.7, $P = 0.01$; Table 7). We found similar patterns of higher mass gains in the fall than in the spring in Ovenbirds ($t = 2.19$, df =

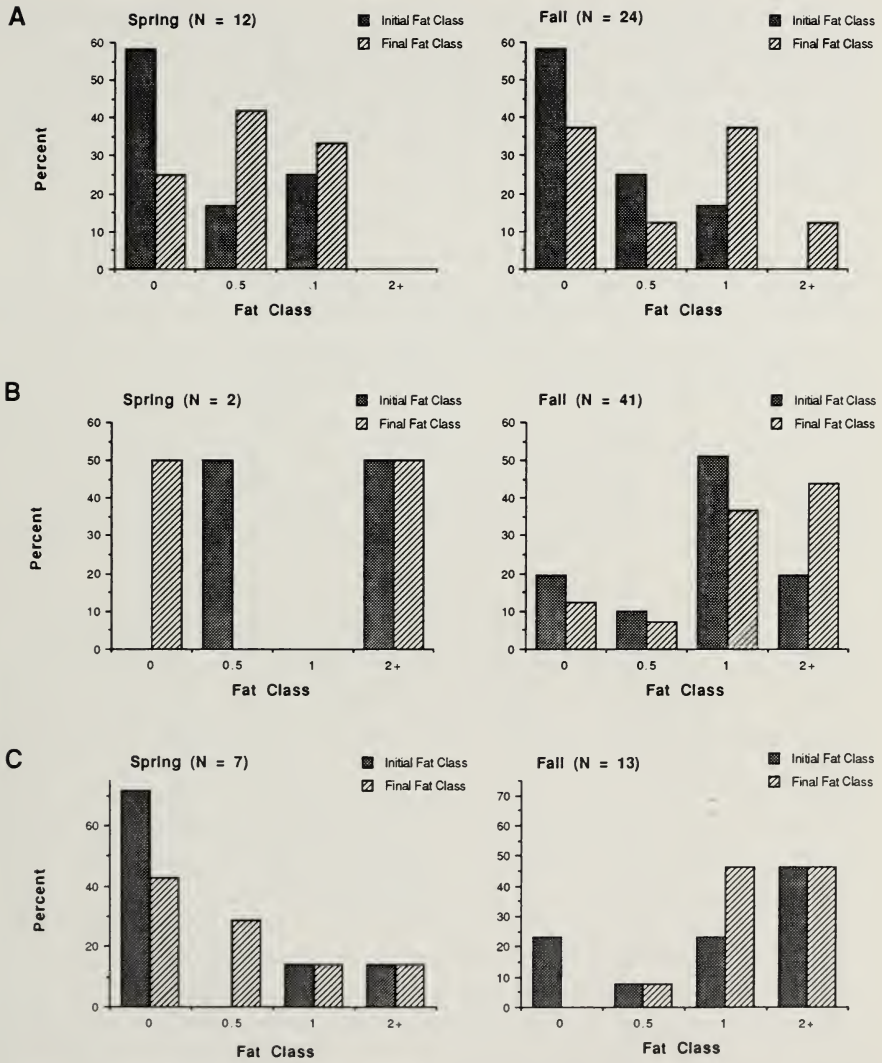

FIG. 2. Changes in the distribution of fat classes between initial and final capture by migrants stopping over on Appledore Island, Maine. A. American Redstart. B. Northern Waterthrush. C. Ovenbird.

15.7, $P = 0.044$) and American Redstarts ($t = 2.30$, df = 30.2, $P = 0.029$).

Paired t-tests on the difference between initial and final mass further assessed the change in body mass during each season. All migrants com-

Table 7

Comparison of Weight Changes by Warblers during Spring and Fall Migration on Appledore Island, Maine

	Spring			Fall		
	N[a]	Percent increase[b]	Daily percent increase[c]	N[a]	Percent increase[b]	Daily percent increase[c]
Magnolia Warbler	12	2.5 ± 9.3	−1.3 ± 5.1	0		
Chestnut-sided Warbler	0			4	5.9 ± 8.1	3.0 ± 3.0
Blackpoll Warbler	0			4	−2.1 ± 6.2	−2.1 ± 6.2
Black-and-white Warbler	3	11.9 ± 17.2	1.3 ± 4.6	9	6.6 ± 11.5	1.5 ± 3.6
American Redstart	12	0.5 ± 7.1	−0.5 ± 3.8	24	7.2 ± 10.3*	1.1 ± 4.7
Ovenbird	7	3.8 ± 4.1	1.4 ± 1.7	13	12.4 ± 13.1*	1.8 ± 1.9*
Northern Waterthrush	2	1.3 ± 10.6	0.2 ± 1.8	41	8.1 ± 8.6*	2.6 ± 2.7*
Canada Warbler	3	1.1 ± 6.4	1.1 ± 6.4	2	−8.2 ± 10.3	−2.2 ± 2.4
Total	39	2.5 ± 8.4	−0.1 ± 2.5	116	6.9 ± 10.0*	1.7 ± 3.5*

[a] Number of individuals recaptured.
[b] Percent gain = (100 × final mass − initial mass)/initial weight.
[c] Daily percent gain = (100 × final mass − initial mass)/initial weight)/length of stopover.
* Significance at $\alpha = 0.05$ level after sequential Bonferroni correction for multiple *t*-tests between weight change and zero.

bined exhibited significant mass increases during both seasons (spring: $t = 1.90$, df = 38, $P = 0.033$; fall: $t = 7.35$, df = 115, $P < 0.001$). The Ovenbird was the only species that experienced a significant average increase in mass during the spring ($t = 2.47$, df = 6, $P = 0.024$). In the fall, Ovenbirds ($t = 3.42$, df = 12, $P = 0.003$), Northern Waterthrushes ($t = 6.03$, df = 40, $P \leq 0.001$), and American Redstarts ($t = 3.43$, df = 23, $P = 0.001$) experienced significant increases in mass.

Because migrants tend to have longer stopovers in the fall than in the spring we also compared daily percent increases between the seasons. Migrants stopping over on Appledore Island gained a significantly higher percentage of mass on a daily basis in the fall than in the spring ($t = 2.59$, df = 58.5, $P = 0.012$; see Table 7). During spring migration, migrants did not exhibit daily percent increases in mass ($t = -0.19$, df = 38, $P = 0.854$). However in the fall, daily percent increases in mass were significant ($t = 5.38$, df = 115, $P < 0.001$). Migrants showed no significant difference in daily mass gain between species in either the spring or the fall (spring: $F_{5,32} = 0.50$, $P = 0.773$; fall: $F_{6,88} = 1.56$, $P = 0.168$).

DISCUSSION

Differences in stopover behavior may be influenced by a number of factors, including distance left to travel during migration (Bairlein 1985, Moore and Kerlinger 1987), time in the annual cycle (Lavee et al. 1991), initial energetic condition (Cherry 1982, Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Loria and Moore 1990, Kuenzi et al. 1991), location of a stopover site in relation to an ecological barrier (Moore and Kerlinger 1987, 1991; Winker et al. 1992a), and suitability of a stopover site, including adequacy of a food supply and competition (Hansson and Pettersson 1989, Kuenzi et al. 1991, Moore and Yong 1991, Moore and Simons 1992). These factors may result in differences in stopover patterns (differences in recapture rates and observed lengths of stopover) not only between seasons but between species and even between individuals and sexes. Although we discuss the data here from the standpoint of single factor analysis, we are aware that certain factors may be additive or confounding in their effects on migration.

We observed different patterns of stopover on Appledore Island between spring and fall migration, both in terms of the proportion of individuals recaptured and length of stopover. Although in this study we encountered more migrant warblers during spring migration (Table 1), both in overall numbers and in terms of individuals captured per net-h, the fall migration yielded more American Redstart and Northern Waterthrush recaptures and longer stopovers in Ovenbirds and Canada Warblers (Tables 2 and 3). Although these results are similar to those of Rabol and

Petersen (1973) in Denmark and Lavee et al. (1991) in the Sinai, Rappole and Warner (1976) reported higher recapture rates in spring than in fall migration for several passerine species (e.g., Nashville Warbler, Ovenbird, and Mourning Warbler) stopping along the Gulf coast. Both distance from the initial point of departure (Abramsky and Safriel 1980) and distance to final destination (Bairlein 1985, Moore and Kerlinger 1987) have been suggested as factors affecting the probability of stopover by migrants. The warbler species encountered on Appledore Island have breeding ranges which extend into New England and Canada. While the northernmost wintering grounds of some migrant warblers are in southern Florida, winter ranges for all of the Appledore migrants extend into central America and the West Indies or South America. Furthermore, although several species have breeding grounds which extend into the southern United States (e.g., Black-and-white Warbler, Ovenbird, and American Redstart), individuals encountered on Appledore Island are most likely breeding in New England or eastern Canada. Therefore, migrants captured during spring migration are farther from their point of initiation of spring migration (at least 1700 km away) than they are to their final destination (which could be 10 to 200 km away). Likewise, migrants captured on Appledore Island during fall migration are closer to the point of initiation than they are to their final destination. The higher recapture rates of American Redstarts and Northern Waterthrushes and longer stopovers of Ovenbirds and Canada Warblers on Appledore in the fall indicate that migrants may exhibit more stopover behavior (e.g., more recaptures and longer stopover periods) early in migration and close to the point of migration initiation. However, the location of a stopover site in relation to an ecological barrier may be as important as its location relative to breeding and wintering grounds.

Appledore Island is positioned at the edge of a major ecological barrier, the Atlantic Ocean. The nearest point of land is only 10 km away and lies directly north (Fig. 1). During fall migration, migrants encountering Appledore Island are assumed to be headed south and thus will see only water. Therefore, migrants must either prepare for barrier crossing or reorient in some way, perhaps by returning to the coastline. During spring migration, northbound migrants encountering Appledore can still see land in their seasonally correct direction, north, and thus may not be likely to interrupt migration by an extended stopover. Spring migrants also may be continuing movement north without undertaking true migratory flights to find suitable food sources and less competition. Movements similar to this were reported by Riddiford and Auger (1983) in Kent. Such movements would result in a lower perceived proportion of individuals exhib-

iting stopovers because individuals would not be recaptured but may have flown the 10 km to the mainland without continuing migration.

A significant finding of this study related to age groups was the high proportion of young birds captured in the spring. Although high proportions of young birds have been documented along the coast in the fall (Baird and Nisbet 1960, Drury and Keith 1962, Murray 1966, Morris 1993), similar ratios heretofore have not been documented in the spring. Because inland stations have lower percentages of young migrants (regularly 60–75%) compared to coastal stations, Ralph (1981) suggests that high proportions of young individuals (90% or more) may indicate the periphery of a species' migratory route. Following this rationale, the high percentage of young individuals captured on Appledore Island during the spring may indicate that most migratory routes are farther inland. A notable exception to the above pattern is the American Redstart which had a much lower proportion of young individuals captured than other species (Table 4). This increased proportion of adults in the population could indicate that during spring migration American Redstarts are following a different migratory path than most other migrant warblers in the northeast. Such a difference in their migratory path could result either from their flying northward and staying along the coast or from their following an inland route north and then changing their heading to the northeast to reach northeastern breeding grounds.

Differences also exist between adults and juveniles during fall migration. Young Northern Waterthrushes were more likely to be recaptured and young American Redstarts had longer stopovers than adults in the fall. The higher recapture rates and longer stopovers among young birds compared to adults in this study are consistent with Ellegren's (1991) study of Bluethroats (*Luscinia s. svecica*) in Sweden. Drury and Keith (1962) suggested that a high percentage of young birds along the coast could be due to hesitation or indecision by young birds encountering a large body of water compared to the continuation of migration over water by adults. This suggestion may in part explain the difference in recaptures and stopover lengths as well. An alternative explanation for the longer stopovers by young birds might be that young birds are not physiologically prepared to initiate a barrier crossing; however, small samples did not permit examination of this hypothesis.

Data presented here indicate a seasonal difference in patterns of stopover between the sexes of Magnolia Warblers. The results show that during spring migration females were significantly more likely to be recaptured than males, but in the fall, there was no significant difference in the rate of recapture between the sexes. Stopovers of several days would result in a delayed arrival at the breeding grounds compared to other

individuals migrating at the same time. Because males often arrive at breeding grounds before females to obtain and establish quality territories (Francis and Cooke 1986), males may be more motivated to continue migration in the spring than females. However, in the fall both sexes may have the same priorities, as both males and females of many species of migrant warblers defend winter territories against all conspecifics (Rappole and Warner 1980). The reported absence of a significant difference in the probability of stopover between the sexes in any species of warblers in the fall may reflect these similar priorities.

Blackpoll Warblers and Magnolia Warblers captured on Appledore were significantly leaner in the fall than in the spring. These results differ from the findings of other studies. Studying trans-Saharan migrants in the Sinai, Safriel and Lavee (1988) found that most migrants were fat-depleted in the spring, and that mass/wing length ratios tended to be lower in the spring than in the fall. Biebach (1985) and Gwinner et al. (1988) suggest that the suppression of migratory restlessness, and thus the probability of stopover, are critically affected by both the energetic conditions of a migrant and the possibility of increasing mass at that stopover site. Therefore, one would expect to recapture more migrants with low fat stores than migrants with high fat stores. At this site, Blackpoll Warblers were leaner in the fall than in the spring and a higher proportion (and more individuals) of this species were recaptured on Appledore Island in the fall.

Our results indicate that migrant warblers tend to increase fat stores and mass during stopover on Appledore Island during both spring and fall migration, but these increases are significant only in the fall (Fig. 2 and Table 7). Data presented here also show that migrants gain significantly more mass during stopovers on Appledore in the fall than in the spring. Bibby and Green (1983) and Moore and Kerlinger (1987) suggest that significant increases in mass by migrants is an indication that an area is a suitable stopover site. Additionally, Winker et al. (1992b, c) and Weisbrod et al. (1993) have shown that habitat use by migrants during stopovers differs seasonally. Therefore, differences in the mass and fat changes between seasons may indicate that the shrub habitats of Appledore Island provide a suitable stopover site for American Redstarts, Ovenbirds, and Northern Waterthrushes in the fall, but in the spring, food may be less available and competition may be increased.

ACKNOWLEDGMENTS

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WADING BIRD USE OF LAKE OKEECHOBEE RELATIVE TO FLUCTUATING WATER LEVELS

Peter G. David[1]

Abstract.—We surveyed the Lake Okeechobee littoral zone by helicopter between 1977 and 1988 to determine wading bird abundance relative to lake water levels. More birds foraged when nesting season (January–July) water levels were below 4.4 m (mean sea level) compared to higher lake levels. Wading birds were also more abundant when nesting season water levels declined by at least 30 cm over the previous two-month period in comparison to more gradual declines or increases in lake levels. Lake levels and change in lake levels over the previous two-month period explained 60% of variation in wading bird abundance. Nesting effort did not appear to be affected by changes in water levels. However, fewer nesting attempts were observed when lake levels were above 4.9 m or below 3.9 m. Peak numbers of nesting wading birds occurred in April and May when lake levels were between 3.9 m and 4.4 m. In general, nesting effort declined during the survey period from over 6000 nests in 1977 and 1978 to between 725 and 1812 nests during the last five years of the study. One possible explanation for this decline is the impact of higher water levels due to increased rainfall and a change in the Lake Okeechobee regulation schedule. Higher water levels reduced the foraging area available to nesting birds and may have contributed to the deterioration of nesting sites comprised of willows. *Received 13 Aug. 1993, accepted 20 March 1994.*

Wading bird populations of the Everglades, including Lake Okeechobee, have declined through the loss or alteration of wetland habitat (Ogden 1978). Changes in wetland hydropatterns, including the timing, duration, and depth of inundation may severely impede the ability of wading birds to forage and reproduce successfully. Shortened hydroperiods can decrease the availability of prey (Loftus et al. 1987), and nesting colonies located in shorter hydroperiod marshes may be exposed to greater nest predation (Frederick and Collopy 1988). Wading birds require a narrow range of water depths in which to forage efficiently (Kushlan 1974, Custer and Osborne 1978), and receding water levels prior to and during nesting are important to concentrate food organisms and create successful foraging conditions in the Everglades (Kushlan et al. 1975, Kushlan 1976).

The South Florida Water Management District (SFWMD) initiated monthly aerial surveys of Lake Okeechobee in 1977 to monitor the effect of the 1978 lake regulation schedule increase on wading bird populations. This paper establishes relationships between lake levels and wading bird use from twelve years (1977–1988) of surveys and supplements previous reports for surveys conducted between 1977 and 1981 (Zaffke 1984) and 1988 (David et al. 1989).

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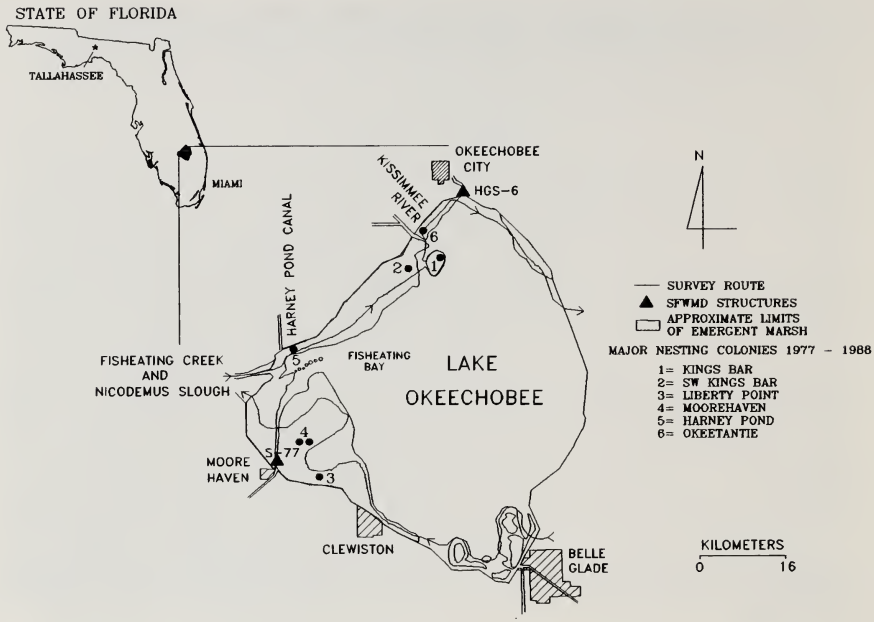

FIG 1. Location of Lake Okeechobee study area, survey route, and major nesting colonies for the period 1977 through 1988.

METHODS

Lake Okeechobee encompasses 1893 km^2 of fresh water in southcentral Florida (Fig. 1), including a 390 km^2 littoral zone located primarily along the western shore between Clewiston and the Kissimmee River (SFWMD 1989). The plant communities within the littoral zone are dominated by cattail (*Typha* sp.); mixed grasses, beakrush (*Rhyncospora* spp.), spikerush (*Eleocharis cellulosa*), and bulrush (*Scirpus californicus*) are also prevalent (Richardson et al. 1991). Willows (*Salix caroliniana*), an important wading bird nesting habitat, occur on elevated ridges (above 4.3 m) in the littoral zone. Willows also are prominent on Kings Bar, an island situated at the mouth of the Kissimmee River, where wading birds historically established large nesting colonies (David 1994).

The littoral zone extends lakeward to nearly the 3.0 m contour; the outward extent is limited by a levee encircling the lake, which was constructed at approximately the 4.7 m contour elevation (Zaffke 1984). Located outside the levee on the west side of the lake are two wetland systems, Nicodemus Slough and Fisheating Creek, which drain into the lake and tend to be inundated at higher lake stages. Nicodemus Slough contains 898 ha of emergent marsh mixed with unimproved pasture, and it is owned and managed by the SFWMD. Fisheating Creek is an extensive riverine system encompassing approximately 17,400 ha of privately owned cypress slough, hardwood swamp, emergent freshwater marsh, and upland habitat.

The SFWMD conducted the Lake Okeechobee surveys by helicopter from 75–80 m in altitude on a specified route around the lake littoral zone marsh, Nicodemus Slough, and Fisheating Creek (Fig. 1). I selected a flight pattern that maximized visibility of the entire

littoral zone. Two observers counted all groups of birds sighted and recorded locations of bird assemblages (≥12 birds) on a map of the lake. Birds were categorized as foraging (i.e., dispersed and feeding in the marsh) or nesting, if assembled in colonies with nests present. Large flocks of foraging or nesting birds were circled several times to improve count accuracy. Total numbers of nests (or nesting pairs) at each colony were recorded. Surveys were designed to establish trends in wading bird abundance relative to water conditions and were not intended to provide a quantitative estimate of bird populations on the lake.

Surveys were conducted at approximately monthly intervals from January 1977 until October 1981, excluding the period of June through September 1978. Beginning in 1982, surveys were completed between April and July when greatest bird use of the lake was anticipated. Four surveys were made each year in 1982, 1983, and 1984; six surveys (February–July) were conducted in 1985 and 1986; seven (January–July) in 1987; and eight (December 1987–July 1988) were completed during the final year of the study, for a total of 93 surveys.

We regularly counted eight species of wading birds during surveys. Great Egrets (*Casmerodius albus*), Snowy Egrets (*Egretta thula*), White Ibises (*Eudocimus albus*), and Woodstorks (*Mycteria americana*) were most visible and I believe were counted most accurately. Darker birds (e.g., Great Blue Heron [*Ardea herodias*], Little Blue Heron [*Egretta caerulea*], Tricolored Heron [*E. tricolor*], Glossy Ibis [*Plegadis falcinellus*]) were more difficult to detect, and their numbers may have been underestimated in the counts. In general, only groups of birds were counted, and scattered individuals, particularly Great Blue and Tricolored herons, were excluded. This resulted in an underestimate of the numbers of feeding birds recorded along the survey route.

Daily water level data were obtained from United States Geological Survey hurricane gauge HGS-6 and the South Florida Water Management gauge at Structure 77, located on the western shore of Lake Okeechobee (Fig. 1). These were considered to be the most representative and accurate gauges for the littoral zone and period of record. Stage elevations used by water managers to operate the Lake Okeechobee system are commonly reported as feet above mean sea level. Lake stages and changes in lake levels presented in this paper have been converted to metric.

I used SAS (1990; version 6.04) to perform analyses on an IBM personal computer. Raw data (numbers of birds foraging and numbers of nests) were log transformed to base 10 to minimize heterogeneity (Zar 1974). I used two-way analysis of variance to test for significant differences in nesting effort among months and change in stage (*d*s) and for interactions between months and stage. I divided lake stages into four treatment levels (1) stages below 3.9 m, (2) stages between 3.9 m and 4.4 m, (3) stages between 4.4 m and 4.9 m, and (4) stages above 4.9 m. Since I made multiple comparisons of stage differences among the seven months of data, Bonferroni's correction for probability levels ($P = 0.05/7 = 0.0074$) was used. I computed multiple regressions to describe the influence of stage and *d*s on wading bird foraging abundance during the nesting season. I calculated squared semi-partial correlation coefficients and associated probability levels for stage and *d*s to determine the relative importance of each of these two variables to the variation in wading bird abundance. This method factored out collinearity which was weak, but a significant correlation ($r = 0.27$, $P < 0.05$) was observed between stage and *d*s.

I used two sets of data. The first included the entire group of monthly survey flights ($N^1 = 93$) for eight species. The second data set incorporated only the nesting season surveys (January–July, $N^2 = 71$) and analyzed data for six species: Great Egret, White Ibis, Snowy Egret, Glossy Ibis, Little Blue Heron, Great Blue Heron, and the total for all six. Wood Storks were included in the analysis of on-lake (littoral zone) and off-lake foraging, while Great Blue Herons were excluded from analysis of off-lake data.

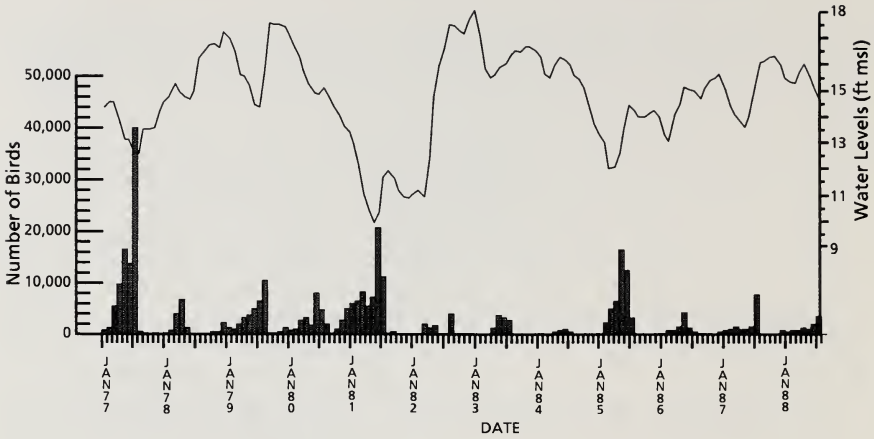

FIG. 2. Total numbers (bars) of birds (foraging and nesting) vs water levels (line) at Lake Okeechobee for the period January 1977 through July 1988.

RESULTS

Wading bird use of the lake varied considerably in relation to fluctuating water conditions, which ranged from drought in 1981 to extremely high water levels in 1979, 1980, and 1982 (Fig. 2). In general, the greatest abundance of foraging wading birds occurred on the lake in the spring or summer when water levels had receded to 3.9 m or lower. For example, in 1977 water levels declined gradually from around 4.4 m in January and February to well below 3.9 m in June and July, which attracted large numbers of wading birds to the lake. In contrast, water levels were extremely high (exceeding 5.2 m) in 1979 and 1980 following implementation of the higher Lake Okeechobee regulation schedule and above average rainfall. In general, these years were characterized by higher numbers of birds feeding off-lake (Fisheating Creek and Nicodemus Slough), with few birds observed on the lake until stages had declined below 4.6 m.

Rapid declines in water levels over a two-month period were associated with greater abundance ($P < 0.01$) of foraging wading birds on the lake during the nesting season (Fig. 3). A two-month decline of between 30 cm and 91 cm in lake levels corresponded to maximum bird counts in July 1977 (39,017 birds), June 1981 (20,620 birds), and May 1985 (15,125 birds). Less distinct differences were detected for total numbers of birds when comparing change in water levels over a two-week or one-month period.

Lake levels were correlated negatively ($r = -0.54$, $P < 0.01$) with

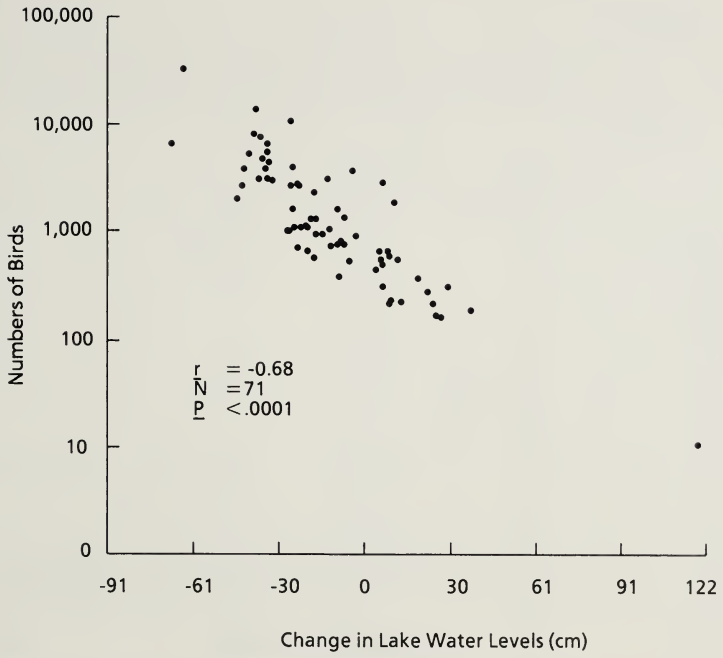

FIG. 3. Relationship between numbers of birds foraging during the nesting season (January–June) and changes in lake levels (cm) at Lake Okeechobee over the two-month period preceding each monthly survey.

wading bird abundance during the nesting season (Fig. 4). Lake levels below 3.3 m continued to provide favorable foraging conditions in the littoral zone along the drying edge of the lake. Wading birds were twice as abundant at these low water levels compared to lake stages above 4.6 m.

Multiple regression equations indicated that water level and changes in water level (*d*s) were significant ($P < 0.05$) predictors of abundance and explained from 25 to 49% of the variation in wading bird abundance among the six species (Table 1). The change in stage over a two-month period was a more important determinant of Great Egret and Little Blue Heron abundance than was lake level. For Snowy Egret, White Ibis, and Wood Stork, stage was a more important variable predicting abundance than the two-month change in water levels. Stage and *d*s explained 60% of the variation in total wading bird abundance with *d*s being a more important predictor than lake level. Similarly, wading bird abundance for all months ($N^1 = 93$) varied with lake levels and *d*s, but these differences were less definitive.

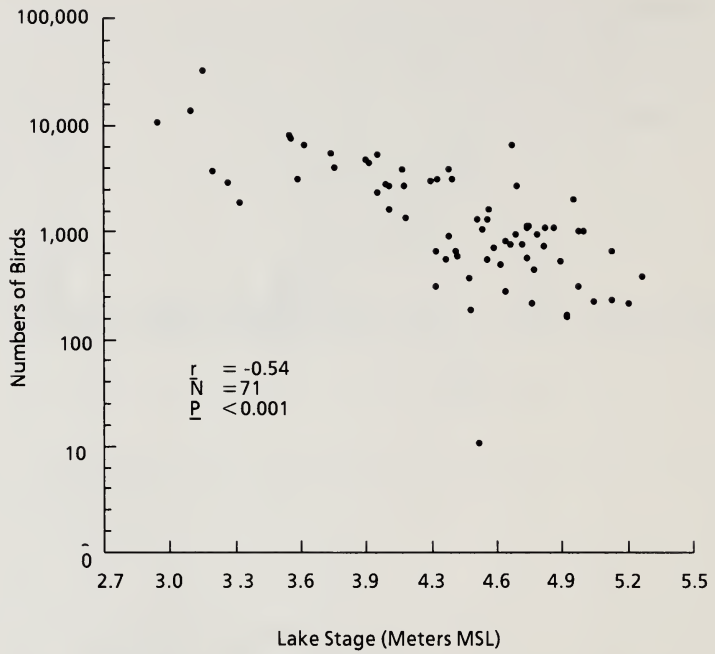

FIG. 4. Relationship between numbers of birds foraging during the nesting season (January–June) and Lake Okeechobee stage.

Using the regression equation to relate total wading bird abundance to stage and *d*s over the previous two months, surface response curves were produced to predict wading bird use on Lake Okeechobee (Fig. 5). Large numbers of wading birds were attracted to the lake at low lake stages, only if water levels had declined rapidly over the previous two months. In addition, these curves indicated that total wading bird use was influenced more by fluctuating lake levels than by stage level.

Temporal changes in wading bird numbers were not evident as two-way analysis of variance revealed no significant differences among the months ($P > 0.5$). There were no significant ($P > 0.5$) interactions between month and *d*s, suggesting that *d*s acted independently in explaining variation in individual and total species abundance.

There were distinct seasonal trends in White Ibis numbers during several years and considerable variation in ibis populations at the lake among years. For example, in 1977 over 19,000 White Ibises were foraging and nesting on the lake through July, but by August most of these birds had emigrated from the lake. Post breeding season exodus of White Ibises also occurred in August or September during the years 1979 through

TABLE 1

REGRESSION COEFFICIENTS FOR COMPARISONS BETWEEN FORAGING ABUNDANCE AND STAGE AND CHANGES IN STAGE (*Ds*) FOR TWELVE NESTING SEASONS (1977–1988) AT LAKE OKEECHOBEE

Species	Total model R^2	Independent variable	Squared semi-partial *r*	P^a
Great Egret	0.49	Stage	0.04	0.0220
		ds	0.35	<0.0001
Snowy Egret	0.33	Stage	0.16	0.0002
		ds	0.09	0.0041
White Ibis	0.44	Stage	0.25	0.0001
		ds	0.09	0.0017
Glossy Ibis	0.26	Stage	0.12	0.0015
		ds	0.08	0.0098
Little Blue Heron	0.25	Stage	0.08	0.0087
		ds	0.10	0.0032
Wood Stork	0.44	Stage	0.26	0.0001
		ds	0.07	0.0046
Great Blue Heron	0.35	Stage	0.31	0.0001
		ds	<0.01	0.6383
Total birds	0.60	Stage	0.14	<0.0001
		ds	0.31	<0.0001

[a] All abundance data was transformed to $\log_{10}$ values prior to analysis. Squared semi-partial R^2 values and probability (*P*) levels are given.

1981, and in July during the years 1984 through 1986. From 1977 to 1981, this species was abundant in the lake vicinity through the breeding season, but during the remainder of the survey period, with the exception of 1985, large numbers of White Ibis were seldom observed at the lake during the nesting season.

Use of Nicodemus Slough and Fisheating Creek by wading birds increased at higher lake water levels. Wading birds were more abundant at off-lake areas during high lake stages than during low lake stages ($P < 0.001$) when all months were included in the data analysis (Fig. 6). Off-lake areas were particularly important to White Ibis, which were observed foraging in large aggregations during August 1977 (8000 birds), December 1977 (6200 birds), and October 1978 (10,180 birds). With the exception of White Ibises, these off-lake areas generally received limited use by other species. However, in May 1983 large numbers of Great Egrets (2065) and Snowy Egrets (2000) were observed in Fisheating Creek and Nicodemus Slough. This occurred following an extended period, beginning in the late summer of 1982 and continuing through the winter of

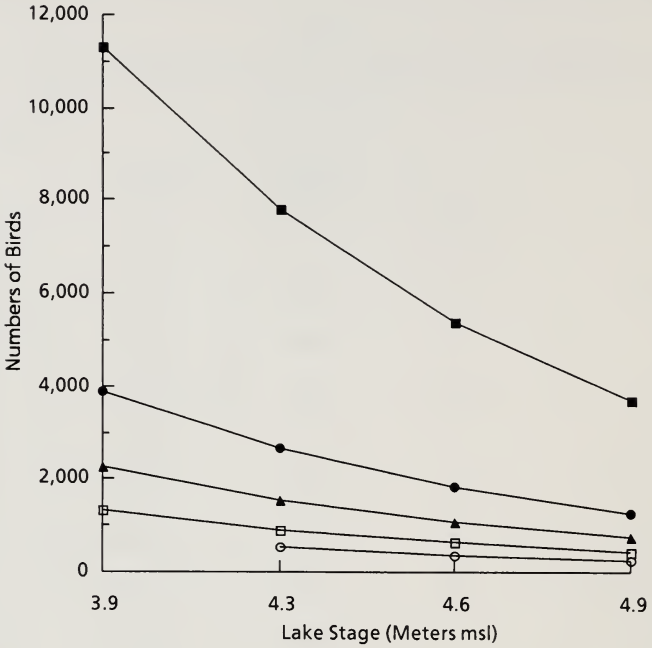

FIG. 5. Simple surface plot predicting total wading bird abundance from Lake Okeechobee stage at five different categories of water level change (over previous two-month period). Solid squares represent change of −61 cm; solid circles represent change of −30 cm; solid triangles represent change of −15 cm; open squares represent no change; and open circles represent change of 15 cm.

1983, when water levels in the lake exceeded 5.2 m. In contrast, only 67 birds were recorded foraging in off-lake areas in 11 surveys conducted between January 1981 and July 1982, which coincided with low lake levels during the drought. Although the low sample sizes precluded statistical comparisons, wading bird use of off-lake areas appeared to be greatest during August and October, with considerably less use occurring during the peak nesting period (March through June).

Twelve different Lake Okeechobee wading bird colony sites were documented. Five of the sites—King's Bar, Liberty Point, Moorehaven, Southwest Kings Bar, and Harney Pond—were used consistently during all or some of the survey years (Fig. 1). Numbers of nesting wading birds, primarily White Ibises and Great Egrets, declined during the survey period from over 6000 in 1977 and 1978 to less than 2000 in 1987 and 1988 (Fig. 7). Although the decline in nesting appeared to be continuous, there were several years characterized by extremely poor nesting effort,

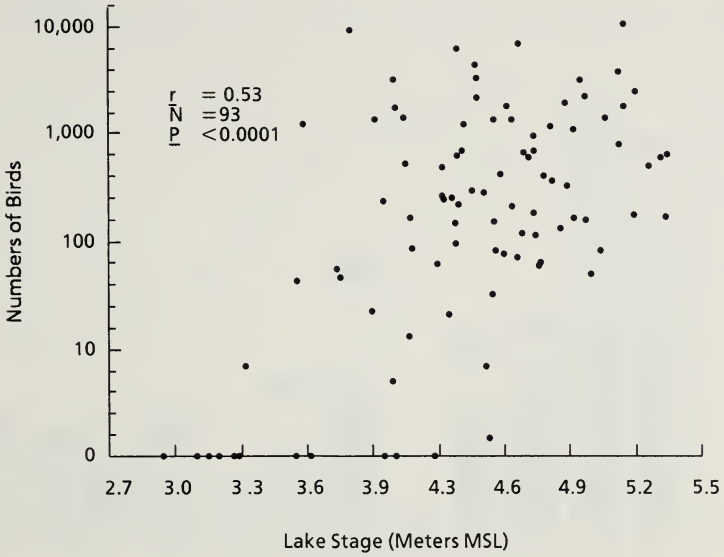

FIG. 6. Relationship between the number of wading birds foraging off-lake and Lake Okeechobee stage for all months ($N^1 = 93$).

including 1981 (520 nests) and 1984 (725 nests), years which had extremely low and high water levels, respectively. Despite favorable water levels and increased foraging activity during the 1985 season, the numbers of wading bird nests increased only slightly. For the remainder of the study period, lake stages remained high (above 4.6 m) throughout the nesting season (1988) or exhibited reversals (i.e., lake water levels increased during the normal dry season recession) during the nesting season (1986 and 1987).

Rate of water level decline did not appear to influence nesting effort, since total nesting effort did not differ significantly ($P > 0.8084$) with *d*s over a two-month period. However, a two-way ANOVA indicated that water levels and month significantly ($P < 0.01$) affected nesting effort such that birds temporally varied nesting effort in response to water levels (Fig. 8). In general, peak nesting occurred when lake levels were between 3.9 m and 4.4 m, compared to higher or lower lake stages. In most years, peak nesting effort occurred in April or May, and dual peaks were observed in 1983 (May and July) and 1987 (March and May).

DISCUSSION

Wading bird foraging and nesting at Lake Okeechobee were related to lake stages and changes in water levels prior to, and during the nesting

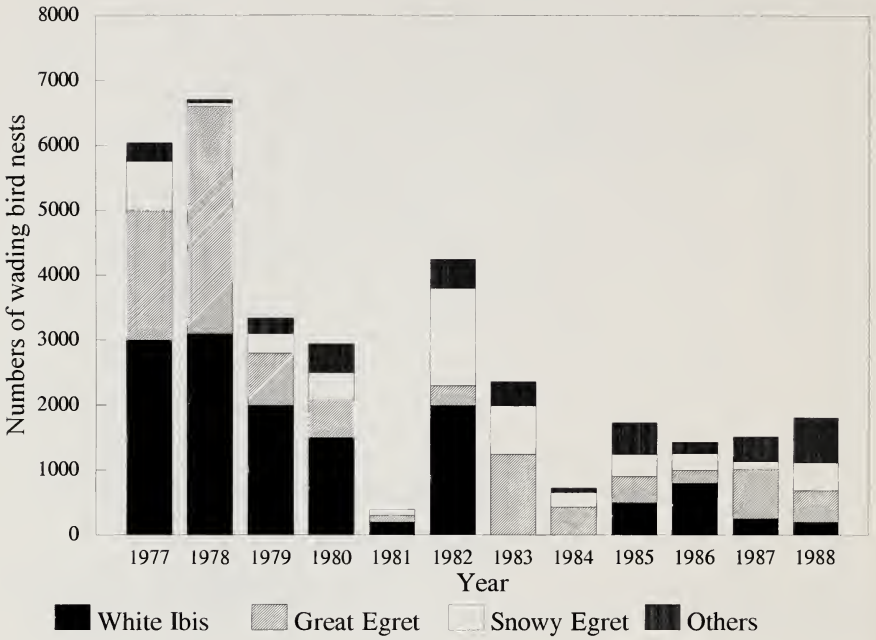

FIG. 7. Maximum numbers of wading bird nests at Lake Okeechobee for each year of surveys. (Others represents Tricolored Heron, Little Blue Heron, Glossy Ibis, and Great Blue Heron nests combined.) Wood Storks did not nest on the Lake during the study period.

period. Nesting wading birds responded favorably to lake levels that were sufficient to inundate littoral marshes, and that then receded to concentrate food in pools along the edge of the exposed littoral zone. A gradual, but continuous receding of lake stage attracted birds to the lake, particularly during the nesting season (January to July). The largest concentrations of birds occurred during dry conditions, indicating that Lake Okeechobee represents critical foraging habitat for wading birds when drought pervades South Florida.

Lake levels may influence the availability of fish and other prey organisms for foraging wading birds. Most wading birds require shallow water (i.e., less than 15 cm for small herons and less than 25 cm for Great Egret and Great Blue Heron) to forage successfully (Custer and Osborne 1978). In addition, Kushlan (1974) indicated that White Ibises avoided foraging in water deeper than 10 cm. Due to the presence of the lake levee, deeper water levels occurred when lake stages exceeded 4.6 m, creating conditions in the littoral zone that were not conducive to wading birds' foraging.

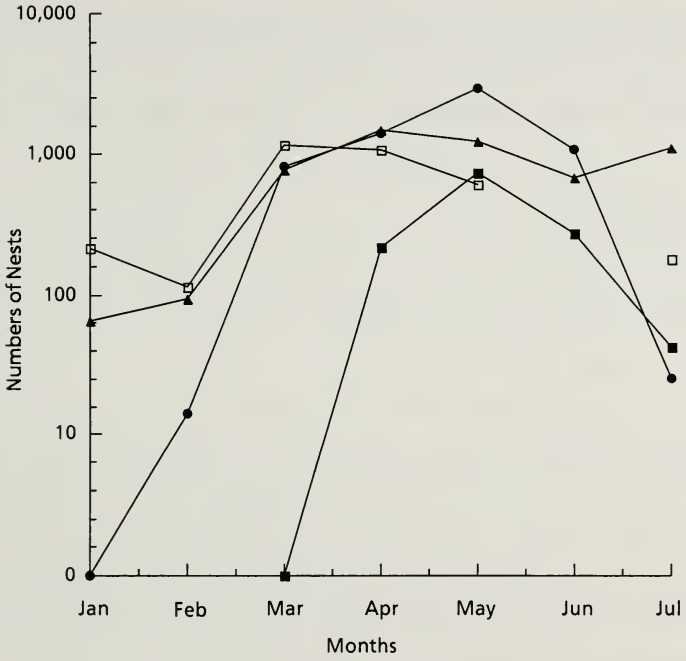

FIG. 8. Relationship between numbers of bird nests by month for four Lake Okeechobee stage categories. Open squares represent stage >4.9 m; solid triangles represent stage between 4.5–4.9 m; solid circles represent stage between 3.9–4.5 m; and solid squares represent stage <3.9 m.

Wading birds were much more likely to use off-lake areas when water levels exceeded 4.6 m. Browder (1976) estimated that the higher lake regulation schedule would reduce by more than 40% the amount of wading bird foraging habitat in the littoral zone. This may be reflected by the movement of White Ibises and Great Egrets from on-lake sites to Nicodemus Slough and Fisheating Creek at higher lake stages. Kushlan (1979) reported that the diet of White Ibises varied, depending on habitat and prey availability, and perhaps being less dependent upon fish in their diet since these birds were able to capitalize on macroinvertebrates in temporarily flooded off-lake areas. Minimal use of off-lake areas during the nesting season by species other than the White Ibis may reflect poor productivity of fish in these short hydroperiod marshes. Loftus et al. (1990) suggested that wetlands may require extended hydroperiods at greater depths to produce larger size classes and sufficient biomass of marsh fish to support wading birds. Consequently, these temporary wet-

lands were less likely to provide high quality forage for Great Egrets and other species which have a diet comprised primarily of fish.

Large concentrations of wading birds in Nicodemus Slough or Fisheating Creek occurred infrequently during the breeding season, regardless of lake levels, suggesting that the remoteness of these areas precluded their use by nesting wading birds. During periods of high lake water levels, nesting birds would have been required to fly at least 30 km from Kings Bar and 10 to 15 km from the Moorehaven colonies to feed in the vicinity of Fisheating Creek and Nicodemus Slough. By comparison, wading birds nesting in the Everglades that were required to fly an average of 27 km to forage were unlikely to reproduce successfully (Bancroft et al. 1990), and foraging flights in excess of this distance may contribute to colony abandonment (Frederick and Collopy 1988).

The survey data indicated a considerable decline in Lake Okeechobee wading bird nesting populations over the course of the study period, which was at least partially due to degradation or loss of dense willow communities as primary nesting sites (David 1994). The decline was most noticeable at King's Bar, which historically had been the largest colony at the lake. Comparisons of lake habitat maps indicated that areal coverage of willow had declined by 35% between the period from 1977 to 1989 (Pesnell and Brown 1977, Richardson et al. 1991). This loss of nesting habitat could account for the poor nesting effort in 1985, despite the large number of birds that foraged at the lake between March and July. In addition, higher water levels may have prompted nesting wading birds to relocate from the large established colony at King's Bar to smaller more remote nesting sites closer to favorable foraging at the lake perimeter (David 1994).

Water management and natural hydrologic conditions can influence wading bird foraging and nesting at Lake Okeechobee. Significantly fewer wading birds foraged on the lake when lake stages were in excess of 4.6 m, suggesting that water levels in the littoral zone were too deep to provide favorable foraging habitat. In contrast, birds were attracted to the lake primarily in the breeding season when water levels exhibited steady decline below 4.6 m. Wading birds avoided nesting under extreme high or low water levels, although fluctuations in water levels did not appear to directly influence whether wading birds nested. The impact of water levels on vegetative community structure influences wading bird reproductive effort. The loss of nesting habitat and the reduction of seasonally inundated wetland communities used by foraging wading birds has probably contributed to the decline in utilization at the lake. Future management plans for the lake should include varying the regulation schedule to allow lake stages to periodically recede (at least every three years) below

3.9 m during the growing season to encourage reproduction and growth of willow communities. In addition, management should provide for the recession of water levels to below 4.3 m beginning in January to create conditions that are more conducive to foraging by nesting wading birds.

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THIRD INTERNATIONAL PENGUIN CONFERENCE

Cape Town, South Africa, 2–6 September 1996

FIRST ANNOUNCEMENT

Following on the successful First and Second International Penguin Conferences held in Dunedin, New Zealand and Phillip Island, Australia in 1988 and 1992, respectively, the Third International Penguin Conference will be held at the Breakwater Lodge, Cape Town, South Africa during 2–6 September 1996.

The conference is being organized by the African Seabird Group, with the support of local organizations and societies, under the broad theme of "Penguins: science and management". It is intended that there will be four days of formal talks and poster sessions, all in plenary, broken in the middle by an excursion to historic Robben Island in Table Bay, home of an expanding population of Jackass or African Penguins *Spheniscus demersus.* Pre- and post-conference excursions are planned to seabird colonies in the West Coast National Park and to a mainland penguin colony on the Cape Peninsula. The proceedings of the conference will be published as a special issue of the African Seabird Group's journal *Marine Ornithology.*

Persons interested in attending should write to the Organizing Committee, Third International Penguin Conference, African Seabird Group, P.O. Box 34113, Rhodes Gift 7707, South Africa, to be placed on the mailing list for the second circular, which it is planned to mail in mid-1995. The second circular will give full details of registration fee, accommodation, excursions, publication plans, etc. It would be helpful if the organizers could be informed of their intent to make a presentation when replying to the first circular. Please also include full postal and electronic mail addresses and an international fax number.

Further information may be obtained from John Cooper, Chairperson of the Organizing Committee, at the above address, or by electronic mail (jcooper@botzoo.uct.ac.za), fax (+27-21-650-3295) or phone (+27-21-650-3294). Other members of the Organizing Committee, from whom information may also be obtained, are Robert Crawford, Bruce Dyer, Norbert Klages and Tony (AJ) Williams.

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SHORT COMMUNICATIONS

The genus *Caryothraustes* (Cardinalinae) is not monophyletic.—The importance of a well-corroborated phylogeny for assessing the evolution of morphological and behavioral traits of birds has been emphasized recently by the analyses of Hackett and Rosenberg (1990), Prum (1990, 1993), Lanyon (1992), Peterson and Burt (1992), and others. Unfortunately, phylogenetic hypotheses at the within-family level are lacking for the vast majority of bird genera and species, and generic allocation of many species is not based on explicit hypotheses, much less data.

The genetic analyses of Tamplin et al. (1993) indicated that the Yellow-shouldered Grosbeak, currently known as *Caryothraustes humeralis,* was not closely related to other cardinaline grosbeaks and perhaps not to cardinalines as a whole. Unfortunately, they did not have access to genetic material of the other two species currently in the genus *Caryothraustes,* both of which are superficially similar to *C. humeralis* in having large, thick bills, black face patterns, and plumage predominantly greenish-yellow and gray. Recent availability of genetic samples of the Yellow-green Grosbeak (*C. canadensis*) permits us to assess the monophyly of the genus *Caryothraustes.* The other species (Black-faced Grosbeak *C. poliogaster*) is extremely similar to *C. canadensis* and differs from it primarily in having gray rather than yellow belly and undertail coverts. *Caryothraustes canadensis* and *C. poliogaster* are allospecies whose close relationship has never been questioned; in fact, Paynter (1970) considered them conspecific. To make our analyses comparable to those of Tamplin et al. (1993), we used protein electrophoresis.

Materials and methods.—Specimens were chosen from representatives of genera within the Cardinalinae as follows: *Caryothraustes humeralis* (Louisiana State Univ. Museum of Natural Science frozen tissue number B-9328), *C. canadensis* (B-1413, B-1414), Northern Cardinal (*Cardinalis cardinalis*) (B-2339), Blue-black Grosbeak (*Cyanocompsa cyanoides*) (B-4871), Rose-breasted Grosbeak (*Pheucticus ludovicianus*) (B-3345), Slate-colored Grosbeak (*Pitylus grossus*) (B-9662), Streaked Saltator (*Saltator albicollis immaculatus*) (B-5254), and Dickcissel (*Spiza americana*) (B-16822). These taxa were chosen to represent evenly the clades depicted in the parsimony tree for Cardinalinae reported by Tamplin et al. (1993). The monotypic genera *Periporphyrus* and *Rhodothraupis* were not included because tissue samples were not available. The non-cardinaline emberizid Plush-capped Finch *Catamblyrhynchus diadema* was used as an outgroup in all phylogenetic analyses. Voucher specimens and frozen tissues are housed in the Louisiana State Univ. Museum of Natural Science.

Homogenates of pectoral muscle were prepared following the methods of Selander et al. (1971). Procedures for starch-gel electrophoresis followed Selander et al. (1971) and Harris and Hopkinson (1976).

Twenty presumptive gene loci were surveyed: adenosine deaminase (ADA, Enzyme Commission number 3.5.4.4); adenylate kinase (AK, 2.7.4.3); aldolase (ALD, 4.1.2.13); alpha-glycerophosphate dehydrogenase (αGPD, 1.1.1.8); creatine kinase (CK, 2.7.3.2); glucose phosphate isomerase (PGI, 5.3.1.9); glutamate-oxaloacetate transaminase (GOT-1, GOT-2, 2.6.1.1); isocitrate dehydrogenase (IDH, 1.1.1.42); lactate dehydrogenase (LDH, 1.1.1.27); malate dehydrogenase (MDH-1, MDH-2, 1.1.1.37); malic enzyme (ME, 1.1.1.40); mannose phosphate isomerase (MPI, 5.3.1.8); peptidase (PEP-B, leucyl-glycyl-glycine; PEP-C, leucyl-alanine; 3.4.11); phosphoglucomutase (PGM, 2.7.5.1); 6-phosphogluconate dehydrogenase (6-PGD, 1.1.1.44); sorbitol dehydrogenase (SODH, 1.1.1.14); and hemoglobin (Hb).

Allozyme data were analyzed using phenetic and phylogenetic approaches. Nei's (1978)

genetic distances (*D*) were generated using the BIOSYS-1 program of Swofford and Selander (1981). To determine the most suitable method of phenetic analysis, the distance matrix was tested for evolutionary rate heterogeneity using both the Fitch and Kitsch programs of PHYLIP (Felsenstein 1993). The Fitch program constructs a phenogram using the Fitch-Margoliash method (Fitch and Margoliash 1967) and does not assume an equivalent molecular clock acting across all lineages. The Kitsch program uses a similar algorithm but assumes equal branch lengths; thus, any incongruence between results of these two methods may indicate the presence of some degree of rate heterogeneity (Felsenstein 1990) and precludes UPGMA clustering which was used by Tamplin et al. (1993). A suitable alternative is the neighbor-joining method of Saitou and Nei (1987), which makes no assumptions concerning evolutionary rates. Archie et al. (1989) demonstrated the necessity of large sample sizes when performing phenetic analyses, contrary to findings of Gorman and Renzi (1979). However, the priority may shift from large sample sizes to increased numbers of characters in phylogenetic analyses (Kesner 1994). Furthermore, scarcity of suitable tissues for members of *Caryothraustes* precludes large samples.

Phylogenetic analysis was conducted using the programs PAUP (Swofford 1993), FREQPARS (Swofford and Berlocher 1987), and MacClade (Maddison and Maddison 1992). An exhaustive search was performed using PAUP to determine minimum-length trees with the loci coded as characters and the alleles coded as character states. MacClade was used to determine the length of alternative tree topologies including that of the distance phenogram. MacClade was also used to determine the length of trees with forced monophyly of *Caryothraustes.*

FREQPARS is a useful program for investigating allozyme data because it assigns each internal node a realistic allele frequency (Swofford and Berlocher 1987). However, it cannot perform branch-and-bound searches (Hendy and Penny 1982) and thus cannot guarantee that all minimum-length trees are found. Therefore, following the method of Page (1990), we generated minimum-length trees using PAUP and entered them as user trees into FREQPARS for comparison. We compared all minimum-length parsimony trees and the distance phenograms using this method.

Results.—Eleven of the 20 loci surveyed here were polymorphic (Table 1). The two individuals of *Caryothraustes canadensis* were identical allozymically; therefore, only one was included in all other analyses. *Caryothraustes humeralis* differed from *C. canadensis* at seven of the 20 loci examined (Nei's $D = 0.431$). The genetic distances separating all other genera within Cardinalinae ranged from 0.180 to 0.531 (mean = 0.377).

The topologies of the Fitch and Kitsch trees were dissimilar, thereby suggesting heterogeneity of evolutionary rates among lineages. Therefore, cluster analysis of the distance data was performed using the neighbor-joining program of PHYLIP. The resulting phenogram (Fig. 1A) indicates that the two species of *Caryothraustes* are not more similar to each other than they are to other genera within Cardinalinae. Also, neither Fitch nor Kitsch trees depict *Caryothraustes* as sister taxa.

Parsimony analysis yielded 10 minimum-length trees with 34 steps and a consistency index of 0.783 (excluding uninformative characters). These 10 trees differed from each other concerning the arrangement of *Cardinalis, Pheucticus,* and *Caryothraustes canadensis,* and a 50% majority-rule consensus tree clearly shows that *Caryothraustes* is not monophyletic (Fig. 1B). There are 2334 trees that are one step longer than the minimum length trees, and the shortest tree depicting *Caryothraustes* as monophyletic is two steps longer (6%) than the shortest trees. The topology of the neighbor-joining phenogram is included among the 2334 near-minimum-length trees with 35 steps.

When analyzed during FREQPARS, all parsimony trees had a length of 66 steps and were shorter than the neighbor-joining phenogram (67 steps). The tree constructed by FREQ-

Table 1

Allelic Variation at 11 Polymorphic Loci in Eight Representatives of Cardinalinae and the Outgroup

Taxon	Locus										
	ADA	ALD	GPD	GOT-1	IDH	LDH	PEP-B	PEP-C	PGD	PGM	Hb
Caryothraustes humeralis	c	b	a	b	b	a	d	d	c	b	a
C. canadensis	a	c	a	a	d	a	b	f	c	a	a
Cardinalis cardinalis	c	a	a	a	e	a	e	c	c	a	a
Cyanocompsa cyanoides	c	b	a	a	c	a	a	h	c	ab	a
Pheucticus ludovicianus	c	b	c	a	c	b	b	i	c	a	a
Pitylus grossus	e	a	a	a	f	a	b	a	b	b	a
Saltator albicollis	e	b	b	a	f	a	a	e	b	b	a
Spiza americana	c	b	b	a	f	a	c	g	d	ab	b
Catamblyrhynchus diadema	c	d	a	a	a	a	d	a	b	a	a

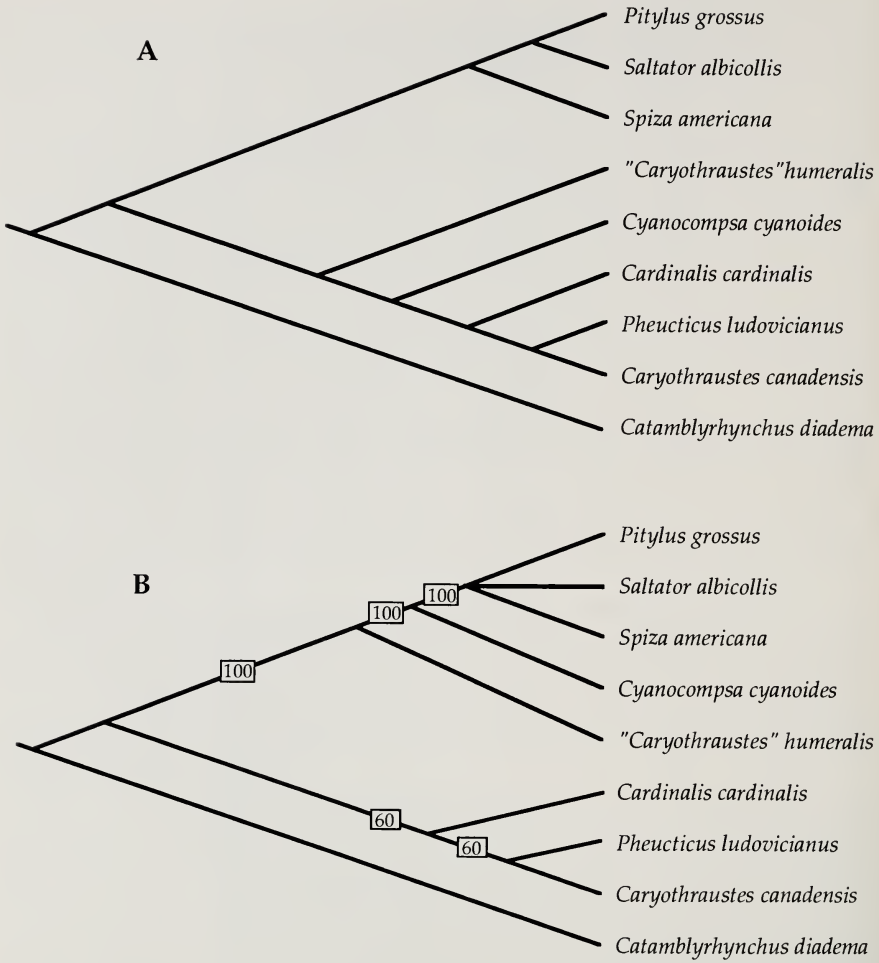

FIG. 1. Neighbor-joining phenogram (A) and fifty-percent majority-rule consensus tree of the ten most parsimonious trees found by PAUP (B) for eight genera of the Cardinalinae and the outgroup. Boxed values on branches leading to clades on the parsimony tree indicate percentage of the ten trees in which the clades were found.

PARS was one step longer than the PAUP trees (67 steps) and showed similarities to both the PAUP trees and the neighbor-joining phenogram. Therefore, all phylogenetic analyses support the 10 minimum-length trees found by PAUP, summarized in Fig. 1B. Importantly, in no analysis (phenetic or maximum-parsimony) was *Caryothraustes* shown to be a monophyletic group.

Discussion.—Based on his examination of external morphology and plumage, Hellmayr (1938:50) long ago noted that *Caryothraustes humeralis* "probably deserves generic separation" from the other two *Caryothraustes* species. Tamplin et al. (1993) summarized an-

ecdotal natural history information that also suggested that *humeralis* was not a member of the genus *Caryothraustes*. The size-corrected morphometric analysis conducted by Tamplin et al. (1993) also failed to support a close relationship between *humeralis* and other *Caryothraustes* species, and, like Hellack and Schnell (1977), Tamplin et al. found that *humeralis* was more similar in morphology and allele frequencies to *Cyanocompsa* than to other cardinalines. Our phylogenetic analysis strongly suggests that *Caryothraustes* is not monophyletic, and that *humeralis* is more closely related to a group of cardinalines consisting of saltators, *Pitylus* grosbeaks, and buntings than to other grosbeaks (including *C. canadensis*) and cardinals.

The species *humeralis* has always been placed in either *Caryothraustes, Pitylus,* or *Saltator* (Hellmayr 1938). The type species for the genus *Caryothraustes* Linnaeus is *C. canadensis*. Our data indicate that *Spiza* and *Cyanocompsa* are more closely related to *Saltator* and *Pitylus* than is *humeralis*. Thus, to allocate *humeralis* to *Saltator* or *Pitylus* would create a paraphyletic genus. Therefore, we are in the process of naming a new genus for *humeralis* (Remsen and Demastes, unpubl. data).

Our analysis of genetic relationships within the Cardinalinae (Fig. 1) supports a previous analysis of allele frequency data (Tamplin et al. 1993) that indicates that the cardinalines may consist of two major clades: (1) the saltators (*Saltator* and *Pitylus*) and Dickcissel (*Spiza*), and (2) the grosbeaks (*Pheucticus*) and cardinals (*Cardinalis*). Placement of the buntings (*Passerina*), grosbeaks of the genera *Cyanocompsa* and *Guiraca,* and other taxa is problematic, and may require the application of higher-resolution techniques (e.g., analysis at the nucleic acid level) to resolve more clearly the phylogeny of the Cardinalinae.

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Genetic structure in a wintering population of American Coots.—American Coots (*Fulica americana*) wintering on the Savannah River Site (SRS), near Aiken, South Carolina, arrive in stages and exhibit temporally stable patterns of site fidelity. Site fidelity in color-marked coots was observed both throughout the winter and across years (Potter 1987) on various portions of Par Pond reservoir on the SRS. In addition, Brisbin et al. (1973) and Potter (1987) found that cesium-137 body burdens of coots differed significantly between

birds from different sites on this reservoir and varied in accordance with the levels of contamination in those sites. These data led us to ask whether the birds from these sites represented distinct and stable population-specific or demographic cohorts which arrived at the reservoir in the same temporal sequence each year and, therefore, were structured on the reservoir with regard to population of origin.

If genetically differentiated breeding populations of coots occupy different sites within a given wintering area, then genetic analyses of the birds on the wintering area should elucidate this structure. Likewise, specific sex and/or age classes of birds from genetically differentiated breeding populations could be detected within a given wintering area. If such populations or sex/age cohorts of coots are mixed on Par Pond, the data should reflect this in two ways. First, there should be a heterozygote deficiency in the overall sample of coots from the reservoir; this is known as the Wahlund (1928) effect. Second, when groups of birds from different breeding areas are categorized correctly on the wintering area, such as site-specific aggregations of birds or sex/age classes, *F*-statistics should indicate that a substantial amount of the total genetic variance is partitioned among these groups within the wintering population. Our objectives were to survey genetic variability in the Par Pond wintering population of American Coots and to use genetic techniques to assess spatial and demographic subsets of these wintering coots in an effort to understand the migratory behavior of this species.

Study area and methods.—Coots were collected from Par Pond, an 1130-ha reservoir on the U.S. Dept. of Energy's Savannah River Site located in Aiken, Allendale, and Barnwell Counties, South Carolina. The reservoir consists of three main extensions which were formed in 1958 by damming the confluence of three adjoining stream systems (Parker et al. 1973). These are referred to as the hot, north, and west arms of Par Pond. A total of 77 birds, 24–27 from each of these arms, were shot on 23 January 1990. Sex was determined by dissection and examination of the gonads and age (1st year, 2nd year, or ≥3rd year birds) was determined from tarsal color (Gullion 1952, Crawford 1978) and/or by examination of the bursa (Eddleman and Knopf 1985). All birds collected showed full tarsal coloration, with no evidence of any of the fading that Crawford (1978) suggested might occur outside of the breeding season. Samples of liver and muscle tissue were removed for electrophoretic analysis and stored at −70°C.

Allozyme electrophoresis was used to estimate genetic variation of each individual. Tissues were thawed and ground with an equal portion of buffer (0.60 gm Tris, 42.8 gm sucrose, 0.45 gm dithiothreitol, and water to equal 500 ml) and centrifuged for approximately 30 sec. The resulting supernatant was screened for variation at 23 presumptive loci, with polymorphisms being consistently resolvable for two loci: PEP-la-1 and PGM (Table 1). Loci were considered variable if the frequency of the most common allele was ≤95%. Each individual was scored for all loci. Buffers and stains are described in Selander et al. (1971), Clayton and Tretiak (1972), and Harris and Hopkinson (1976). Loci were designated numerically beginning with the most anodal. Alleles were designated based on their anodal or cathodal position relative to the most common allele observed. Single and multiple locus heterozygosity, measures of allozyme diversity, were estimated using the computer program BIOSYS-1 (Swofford and Selander 1981). This program was also used to evaluate fit of the data to Hardy-Weinberg expectations and to calculate *F*-statistics (F_{ST}, F_{IS}, and F_{IT}; Nei 1977) for comparisons among birds in the three arms of Par Pond as well as for comparisons between sexes, among ages, and among sex and age classes of coots present in the reservoir. F_{ST} measures the extent to which subpopulations show genetic heterogeneity or more specifically, it indicates the proportion of genetic variation in the total population that is accounted for by the subpopulations. F_{ST} can range from 0 (no differentiation among subpopulations) to 1 (complete differentiation or fixation of alternate alleles). F_{IS} and F_{IT} measure

TABLE 1

PROTEIN ABBREVIATION, LOCUS NAME, ENZYME COMMISSION (E. C.) NUMBER, BUFFER, TISSUE, NUMBER OF ALLELES, AND AVERAGE HETEROZYGOSITY (H) FOR LOCI SURVEYED IN AMERICAN COOTS WINTERING ON THE PAR POND RESERVOIR IN SOUTH CAROLINA

Abbreviations	Locus name	E. C. number	Buffer[a]/tissue[b]	Alleles	h
AAT-1	Aspartate aminotransferase-1	2.6.1.1	AC/M	1	0.00
AAT-2	Aspartate aminotransferase-2	2.6.1.1	AC/M	3	0.03
AH	Aconitate hydratase	4.2.1.3	AC/M	1	0.00
ACP	Acid phosphatase	3.1.3.2	AC/L	1	0.00
ADA	Adenosine deaminase	3.5.4.4	TC8.0/M	2	0.03
FH	Fumarate hydratase	4.2.1.2	AC/L	1	0.00
GPI-1	Glucose-6-phosphate isomerase-1	5.3.1.9	AC/L	1	0.00
GPI-2	Glucose-6-phosphate isomerase-2	5.3.1.9	AC-L	1	0.00
IDH-2	Isocitrate dehydrogenase-2	1.1.1.42	TC8.0/M	2	0.01
LDH-1	Lactate dehydrogenase-1	1.1.1.27	AC/L	2	0.01
LDH-2	Lactate dehydrogenase-2	1.1.1.27	AC/L	1	0.00
LAP	Leucine aminopeptidase	3.4.–.–	AC/L	1	0.00
MDH-1	Malate dehydrogenase-1	1.1.1.37	AC/M	1	0.00
MDH-2	Malate dehydrogenase-2	1.1.1.37	AC/M	1	0.00
ME-1	Malic enzyme-1	1.1.1.38	AC/M	2	0.01
ME-2	Malic enzyme-2	1.1.1.38	AC/M	3	0.08
MPI-1	Mannose-6-phosphate isomerase-1	5.3.1.8	TC8.0/L	3	0.04
MPI-2	Mannose-6-phosphate isomerase-2	5.3.1.8	TC8.0/L	1	0.00
PEP-la-1	Peptidase-leucyl alanine-1	3.4.–.–	AC/L	4	0.10
PEP-la-2	Peptidase-leucyl alanine-2	3.4 –.–	TC8.0/L	1	0.00
PGM	Phosphoglucomutase	5.4.2.2	AC/L	5	0.20
6PGD	6-phosphogluconate	1.1.1.44	AC/L	1	0.00
SORDH	Sorbitol (=L-iditol) dehydrogenase	1.1.1.14	TC8.0/L	1	0.00

[a] Buffers: AC = Amine-citrate pH 6.1; TC 8.0 = Tris-citrate pH 8.0.
[b] Tissues: L = liver; M = muscle.

the heterozygote deficiency or excess relative to the expected heterozygosity within subpopulations (F_{IS}) and the total population (F_{IT}), respectively, and range from −1 to 1. Positive numbers indicate heterozygote deficiency and negative numbers indicate heterozygote excess.

Results.—The mean multilocus heterozygosity of 23 loci for all individuals sampled was 0.021 ± 0.010 (1 SE) and was similar among birds from the three arms of Par Pond. Single locus heterozygosity for all individuals sampled ranged from 0.00 to 0.195 (Table 1). The mean F_{ST} for the comparison of coots among the three arms of Par Pond was 0.01 with only 1% of the genetic variation being partitioned among birds from different portions of the reservoir. A 10–11% heterozygote deficiency was observed within the groups of birds sampled in different portions of the reservoir and for all birds combined (Table 2).

F-statistics calculated for comparisons between sexes and among ages of coots on the reservoir were quite similar to those calculated from analyses of the birds in the three sampling sites. Comparison between sexes indicated that little of the total genetic variation was partitioned between males and females present in the reservoir. Comparison among age

TABLE 2

MEAN F_{IS}, F_{IT}, AND F_{ST} VALUES (NEI 1977) FROM GENETIC ANALYSES OF AMERICAN COOTS COLLECTED FROM THE SAVANNAH RIVER SITE ON 23 JANUARY 1990

Grouping[e]	F_{IS}	F_{IT}	F_{ST}
Capture site[a]	0.097	0.107	0.011
Age[b]	0.075	0.096	0.022
Sex[c]	0.114	0.117	0.003
Sex/age class[d]	0.000	0.065	0.064

[a] Sample sizes for capture sites are 25, 27, and 27 for the Hot, North, and West arms.
[b] Sample sizes for the three age classes are 26, 31, and 22 for year classes 1–≥3.
[c] Sample sizes for the sexes are 47 and 32 for males and females.
[d] Sample sizes for sex/age classes are 14, 14, and 4 for females year 1–≥3 and 12, 17, and 18 males year 1–≥3.
[e] *F*-statistics were calculated for comparisons of all birds among three capture sites, among three age classes (Crawford 1978), between sexes, and among sex and age classes of birds.

classes of coots also indicated that little of the total genetic variation was partitioned among birds in year classes 1, 2, and 3. There were again large heterozygote deficiencies within males, females, and each age class (Table 2). F_{IT} values from the analyses performed between sexes and among ages were also large and indicated heterozygote deficiencies in the total reservoir population. However, when the *F*-statistics were calculated for comparisons among the six sex/age classes (i.e., year 1 males, year 1 females, year 2 males, etc.) there were no heterozygote deficiencies within these groups, but a significant amount (6.5%) of the total genetic variation was partitioned among these groups. The F_{IT} value from this analysis (0.065) was almost identical to the F_{ST} (0.064) as would be expected in an analysis of spatially subdivided randomly mating subpopulations.

Discussion.—The mean heterozygosity of coots on Par Pond (2.1%) was lower than the mean of 6.5% (range 0–30.7%) for 79 other species of birds (Evans 1987) but was similar to that of King Rails (*Rallus elegans*) and Clapper Rails (*R. longirostris*; 3% and 4%, respectively; Avise and Zink 1988). The small F_{ST} (0.011) calculated for the birds from the three sampling locations indicated that very little of the genetic variation was partitioned among the birds located in the Par Pond sampling sites. The F_{IS} and F_{IT} (0.097 and 0.107, respectively) values indicated an overall deficiency of heterozygotes (Wahlund effect) in the samples within each site and for the overall sample. These data suggest that birds from each arm of the reservoir are a mixture of birds from genetically differentiated breeding populations and do not represent specific cohorts from distinct breeding populations.

Data from both sexes and each age class of birds exhibited heterozygote deficiencies and little of the total genetic variance was partitioned among these groups. Although there is evidence for some waterfowl species such as Mallards (*Anas platyrhynchos*) that birds of different ages may winter in different locations (Nichols and Hines 1987:50), our data suggest that the wintering population of coots on Par Pond may be composed of a mixture of sex/age classes from genetically differentiated breeding populations.

A combination of site fidelity and sex/age stratified wintering behavior in American Coots may be responsible for the patterns of genetic structure observed on Par Pond. Site fidelity to wintering grounds is not unique to coots; it has previously been described in Sanderlings (*Calidris alba*; Myers et al. 1979), and Red Knots (*Calidris canutus*; Harrington et al. 1988). Studies by Potter (1987) found that during fall migration coots returned to the three arms of Par Pond sequentially, with numbers peaking first in the west arm, followed by the hot and north arms. Sightings of coots color-marked by Potter (1987) also indicated site fidelity

of individual coots to specific arms of Par Pond across years, with only 2% of 272 sightings of 85 individual coots being outside of the reservoir arm where they had been initially captured during January–February of the same year. During the following winter, only three of 30 sightings of these same coots were not in the same arm where they had been captured originally, and one year later (2 years after initial capture), a single sighting of a marked coot was again in the same reservoir arm where it had been originally captured.

The results of the present study suggest that, rather than population-specific cohorts arriving differentially at Par Pond, there are more likely demographic cohorts such as sex/age classes from different breeding populations that mix randomly across the reservoir. The temporal site fidelity of coots on Par Pond observed by Potter (1987) may reflect the site fidelity of such specific sex/age classes of coots as they return year after year. Sightings of two neck-collared coots, one wintering on Par Pond and another spending two consecutive winters at the same location on another reservoir located approximately 167 km to the north of the Savannah River Site, indicate that at least some of these birds represent a population that breeds in the Horicon March, Wisconsin (D. Rusch, pers. comm.).

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Birds breeding in or beneath Osprey nests in the Great Lakes basin.—Ospreys (*Pandion haliaetus*) build large stick nests, most commonly at the top of dead trees close to, or standing in, water. Material is added to nests each year, and if the supporting branches are strong enough, a nest may reach up to 3 m deep (Bent 1937, pers. obs.). There are scattered reports in the literature of other bird species breeding within occupied Osprey nests or immediately below them (e.g., Bent 1937, Reese 1977, Terres 1991), but many reviews of Osprey ecology do not mention this habit (e.g., Cramp 1980, Henny 1986, Poole 1989). In addition, a variety of open-nesting bird species will breed in unoccupied Osprey nests (e.g., Yocom 1952, Wetmore and Gillespie 1976, Poole 1989). During the course of eco-toxicological work on Ospreys in the Great Lakes basin in 1991 and 1992 (PJE), and during long-term studies of population biology and general ecology of Ospreys in central Michigan since the early 1960s (SP), we recorded a variety of bird species nesting either in Osprey nests or in the supporting structure. In this paper, we present details of these observations, as well as some recent incidental records, and provide a review of the scattered literature relating to this intriguing phenomenon.

Observations during the 1991 and 1992 breeding seasons (mid-April to early August) were made at intervals of 2–4 weeks, while we checked nests in four study areas in Ontario and Michigan. At Ogoki Reservoir (51°N, 88°W), north of Lake Nipigon, all nests were in dead conifer snags in deep water. In the St. Marys River (46°N, 84°W), in NW Lake Huron,

most nests checked were located either in live or dead eastern white pines (*Pinus strobus*) or on metal navigation towers. In SE Georgian Bay (45°N, 80°W), Lake Huron, nests were located mostly on artificial single-pole platforms, old hydro poles, or in dying eastern white pines. In the Kawartha Lakes (44°30′N, 78°30′W), Ospreys used artificial tripod or quadropod platforms, stumps, or dead snags in shallow water. At Fletcher Pond (45°N, 84°W), and other inland floodings in Michigan, nests were located on artificial platforms or dead snags over water.

We inspected the contents of Osprey nests with the aid of climbing equipment, ladders, or mirrors and noted details of any other bird nests or territorial behavior of adults of other species. Since we could not see into all available holes, either in the base of the Osprey nest or in the trunk of a supporting tree, a species was regarded to be nesting if it returned to a cavity after we had moved away from the site.

We recorded six species of small birds (a total of 20 cases) breeding within or immediately beneath occupied Osprey nests in the Great Lakes basin. Nests of Common Grackle (*Quiscalus quiscula*) (8), Tree Swallow (*Tachycineta bicolor*) (6), European Starling (*Sturnus vulgaris*) (1), and House Sparrow (*Passer domesticus*) (2) were noted within Osprey nests themselves, whereas Northern Flicker (*Colaptes auratus*) (one in hole in tree) and Barn Swallow (*Hirundo rustica*) (one in a concrete building in two consecutive years) bred only in the supporting structures. Excepting one site with nesting Tree Swallows at Ogoki Reservoir, Ospreys laid eggs at each occupied nest in which small birds bred. On no occasion did we detect any agonistic interactions between the Ospreys and the other nesting species.

In 1992, we recorded the following incidence of small birds nesting in or beneath occupied Osprey nests: Ogoki Reservoir = 4/14 (29%); St. Marys River = 2/10 (20%); Georgian Bay = 2/26 (8%); and Kawartha Lakes = 5/40 (12%). Overall, 13 of 90 (14%) occupied Osprey nests in 1992 also had small birds breeding in or beneath them. These species nested significantly less often in association with Osprey nests on artificial platforms (2 of 51 nests, 4%) than at natural sites (8 of 27 nests, 30%) ($G_1 = 10.1$, $P < 0.01$). Artificial platforms predominated in Georgian Bay and the Kawartha Lakes, but tree sites were most frequent at Ogoki Reservoir, and navigation aids predominated in the St. Marys River. At artificial platforms, Osprey nests were usually less than 1 m deep, whereas nests in trees, and some on tall metal towers, were often 2–3 m deep, and therefore offered fewer nest sites for small birds.

Seven large bird species bred in nests formerly occupied by Ospreys, involving a minimum of 25 cases. Great Blue Herons (*Ardea herodias*) bred in an unoccupied Osprey nest in the Kawartha Lakes in 1988 and continued to breed there until the nest blew down in 1991. Similarly, an Osprey nest on a tripod platform on Fletcher Pond was occupied by Bald Eagles (*Haliaeetus leucocephalus*) for two seasons after it was vacated by Ospreys (Postupalsky 1978), and one tripod platform there was occupied by Bald Eagles in 1989 after their natural tree nest fell down. In the St. Marys River, in late April 1991, an Osprey occupied what appeared to be a Bald Eagle nest, but by late May the eagles had taken over the site and were incubating. In 1992 and 1993, Bald Eagles again bred there. Red-tailed Hawks (*Buteo jamaicensis*) bred in an unoccupied Osprey tree nest in the Kawartha Lakes in 1982, and in the 1970s, Great Horned Owls (*Bubo virginianus*) (three cases) nested in old Osprey nests on artificial platforms at inland floodings in Michigan. In four cases, Herring Gulls (*Larus argentatus*) built nests on artificial Osprey platforms in Michigan which had not previously been unoccupied by Ospreys. In three instances Great Horned Owls bred in old Osprey nests in trees in Michigan. A pair of Common Ravens (*Corvus corax*) bred in 1990 and 1991 in an unoccupied Osprey nest on a transmission line tower in Georgian Bay.

Canada Geese (*Branta canadensis*) attempted to nest in Osprey nests on artificial plat-

forms at Fletcher Pond and other floodings in Michigan on at least 12 occasions during the past thirty years. In each case the geese were incubating by the time Ospreys returned in early to mid-April. In some cases the displaced Ospreys nested at a nearby alternative site (either another artificial platform, or a low stump), but more often the Osprey pair occupied the platform once the goose clutch hatched, although none of these pairs laid eggs in that same year.

At the St. Marys River, Canada Geese nested among a pile of sticks, which had fallen from an Osprey nest 6 m above, on top of an old navigation beacon. The geese were incubating by the time Ospreys arrived back each year, and were successful in both 1991 and 1992. Although the Ospreys occupied the upper nest in both years, they did not breed successfully in either year. In 1993 the Canada Geese bred elsewhere, and Ospreys bred successfully at this site. In the Great Lakes basin, most Canada Geese hatch eggs in May, just after the mean laying date for Ospreys (PJE, unpubl. data.). We witnessed no aggressive interactions between Canada Geese and Ospreys occupying the same sites, but in the Kawartha Lakes, Canada Geese approaching occupied Osprey nests later in the season were usually attacked fiercely. At one small lake in the Kawartha Lakes area, Canada Geese took over a regularly occupied Osprey nest on an artificial platform in 1988, and have bred there since. There appeared to be no suitable alternative nest sites nearby for Ospreys, so local landowners installed a second platform 400 m away in 1989, but this too was occupied by geese before the Ospreys returned. Since 1989 Ospreys have been seen only foraging occasionally at this lake.

Small birds breeding within or immediately beneath an active Osprey nest may benefit from a decreased risk of predation at the nest because Ospreys attack fiercely any potential predators such as crows, other raptors, and mammals (Bent 1937; Reese 1977; Poole 1989, pers. obs.). However, some potential avian predators were not attacked by some breeding Ospreys (Jamieson and Seymour 1983). Various "weaker" bird species have been recorded nesting around (or in) nests of birds of prey and other "aggressive" species, a phenomenon known as "protective nesting" (see reviews by Durango [1949], and Van Tyne and Berger [1959]). It is possible that in some cases Ospreys also benefit from such nesting associations, since potential predators that escape detection by the Ospreys may be spotted by a small bird breeding beneath. Adult Ospreys are usually alerted by alarm calls of other bird species near their nest (pers. obs.).

There has been some debate as to whether small birds actively select these nest sites because of the additional protection afforded, or simply because suitable sites are available there (e.g., Durango 1949). We suspect that suitable cavities for these six small bird species were not abundant in our study areas. Further, since Ospreys select larger, older, usually dead trees for nesting (due to support required for the large nest), these sites offer a greater number of nesting opportunities for such cavity nesters than are found in younger trees. Bent (1937) also noted that Osprey nests on artificial support structures were shallower than those in trees. Presumably there are more potentially suitable cavities for nesting passerines within the base of Osprey nests in trees, than on artificial platforms. Small birds may also benefit from an increased availability of nest material and insect food. Tree Swallows regularly collect down and feathers from around Osprey nests, and take them to line their nests (pers. obs.). Barn Swallows and Tree Swallows often feed on flying insects around Osprey nests—many insects appear to be attracted by the rotting fish remains (pers. obs.).

There has been no previous extensive review of other birds breeding at Osprey nests. In collating accounts of birds nesting in close association with Ospreys, or in their old nests, we found 14 species of small birds mentioned: Northern Flicker, Lewis' Woodpecker (*Melanerpes lewis*), Western Kingbird (*Tyrannus verticalis*), Tree Swallow, Violet-green Swallow (*Tachycineta thalassina*), Barn Swallow, Short-toed Treecreeper (*Certhia brachydac-*

tyla), House Wren (*Troglodytes aedon*), White Wagtail (*Motacilla alba*), European Starling, a shrike (*Lanius* sp.), Common Grackle, House Sparrow, and European Tree Sparrow (*Passer montanus*) (Allen 1892, Bahr 1907, Abbott 1911, Bent 1937, Moll 1962, Garber 1972, Reese 1977). Most accounts presumably refer to single pairs of small birds, but as many as four (Bahr 1907; Brehn 1878, cited by Moll 1962), and 6–7 (Abbott 1911) pairs of Common Grackle have been found breeding in the base of a single Osprey nest. Abbott (1911) also mentions meadow mice (*Zapus hudsonius*) living in the base of a nest.

Eleven larger bird species have been recorded previously to nest in or beneath Osprey nests: Black-crowned Night-heron (*Nycticorax nycticorax*), Green-backed Heron (*Butorides striatus*), Great Blue Heron, Canada Goose, Mallard (*Anas platyrhynchos*), American Black Duck (*A. rubripes*), Bald Eagle, Peregrine Falcon (*F. peregrinus*), Barn Owl (*Tyto alba*), Great Horned Owl, and Eurasian Jackdaw (*Corvus monedula*) (Allen 1892; Fannin 1894; Abbott 1911; Yocom 1952; Geis 1956; Craighead and Stockstad 1961; Moll 1962; Flath 1972; Garber 1972; Wetmore and Gillespie 1976; Reese 1977; Poole 1989; Campbell et al. 1990; R. H. Dennis, pers. comm.).

Green-backed Herons and Black-crowned Night-Herons have bred among sticks at the base of occupied Osprey nests, as close as 0.5 m from the Ospreys but usually separated by a solid board or dense brush (Allen 1892, Abbott 1911, Reese 1977). Great Blue Herons also breed occasionally in deserted Osprey nests, as the two species nest quite regularly in dead snags on the same beaver ponds; Ospreys will likewise nest in old Great Blue Heron nests (Fleming 1901; Macoun and Macoun 1909; Snyder 1931; Ivanovs 1972; Stocek and Pearce 1978; Ontario Nest Record Scheme, Royal Ontario Museum, Toronto; pers. obs.). In Chesapeake Bay, Mallard laid eggs in Osprey nests, both with and without Osprey eggs, but the Ospreys were rarely successful in such cases (Reese 1977).

The cases we report here of Red-tailed Hawk and Herring Gulls breeding in unoccupied Osprey nests in the Great Lakes basin appear to be the only ones on record. Mathisen (1977) noted three instances of Ospreys taking over unoccupied Bald Eagle nests in Minnesota, but Bald Eagles are usually dominant over Ospreys in areas of sympatry (Bent 1937; Ogden 1975; Poole 1989, pers. obs.). In Wisconsin, Bald Eagles took over two Osprey nests in 1992 which had previously been used by Ospreys (Gieck et al. 1992), but eagle nests in old Osprey sites in trees usually become top heavy and fall down (SP, unpubl. data). Ospreys have been recorded breeding at a few unoccupied Bald Eagle nests in the Great Lakes basin, particularly when eagle populations were severely depleted by the effects of organochlorine contaminants in their food (Ontario Nest Record Scheme, Royal Ontario Museum, Toronto, pers. obs.). Great Horned Owls in Labrador bred in 35 (54%) of 68 Osprey nests checked between 1969 and 1973, and there was some suggestion that in years of high hare and grouse numbers, a greater proportion of Osprey nests were occupied by the owls (Wetmore and Gillespie 1976).

Among non-passerine species, Canada Geese have been reported nesting in Osprey nests most frequently. In the Great Lakes basin we know of no instances of geese breeding in Osprey nests in trees, but this practice has been recorded in other areas, in trees up to 30 m high (e.g., Fannin 1894, Yocom 1952, Craighead and Stockstad 1961, Flath 1972). Mortality of goslings jumping from high tree nests is very low (Craighead and Stockstad 1961). Presumably such sites are attractive to geese owing to a reduced risk of predation. Increasing use of artificial nest platforms by Canada Geese (Craighead and Stockstad 1961, Rienecker 1971, Mullen 1975, cited by Poole 1989, this study) has resulted in increased conflicts with breeding Ospreys, usually in the form of direct take-over of the Osprey nest before Ospreys arrive in spring. In British Columbia, some Ospreys have been prevented from breeding by Canada Geese that breed before Ospreys arrive in spring (Campbell et al. 1990). In Montana, it is only in years when mild weather permits Canada Geese to lay in early March that there

is sufficient time for Ospreys to breed at the same site after the geese have hatched (Flath 1972). similarly, in two of three years at one site in California, Ospreys laid eggs in a nest after Canada Geese had hatched (Garber 1972). Ospreys have been known to evict Canada Geese from nests in trees (Flath 1972), but usually the attacks on incubating geese are unproductive (e.g., Mullen 1985 cited by Poole 1989, pers. obs.).

Clearly, in areas where suitable nest sites are in short supply, increasing Canada Goose populations reduce nest site availability for Ospreys, particularly when goose eggs do not hatch until a month or so after the Ospreys have returned in spring. At some small lakes and floodings in the Great Lakes basin, various measures are currently being considered to prevent geese from breeding on artificial platforms. These include: removal of all nest material after the Osprey breeding season; placement of tall (plastic) objects in the center of the nest scrape; or the covering of the complete nest platform with wooden sheeting or tarpaulins until just after Ospreys return. Although such measures present some logistical problems, on a local scale they would assist with the recovery of those Osprey populations affected by heavy use of organochlorine pesticides during the 1950s, 1960s, and 1970s (Poole 1989).

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Group size and flight altitude of Turkey Vultures in two habitats in Mexico.—The efficiency of carcass exploitation by scavenger guilds is related to patterns of searching and finding carcasses, feeding behavior and the efficiency of one or two species in the guild to find carrion (Alvarez et al. 1976; Attwell 1963; Houston 1974, 1979, 1988; Kruuk 1967; Rodríguez-Estrella 1986). The Turkey Vulture (*Cathartes aura*) is present in every existing scavenger guild (Brown and Amadon 1968) and is perhaps the most important scavenger species due to its efficiency in finding and exploiting carcasses (Houston 1986). Turkey Vultures forage individually or in widely scattered small groups with other vulture species. However, limited information is available on their foraging habits where Turkey Vultures are allopatric with respect to other vultures and variations in group size may be related to the density of the species (Prior 1990). In this study, I analyzed whether the foraging group size of Turkey Vultures was related to population density or to other factors, such as carrion size and availability. The vultures were studied in two areas with similar population density (Hiraldo et al. 1991, this study), different carrion size and availability, and without the presence of other vulture species.

Methods.—I studied vultures in La Michilía (23°20′–23°30′N, 104°07′–104°20′W) and Mapimí (26°29′–26°52′N, 103°58′–103°32′W) Biosphere Reserves at Durango, México. La Michilía is an irregular high plain (elevation 2250 m) between two mountain ranges. The climate is semiarid with summer rains, annual mean precipitation of 567 mm, and an annual mean temperature ranging between 17.4°C and 20.7°C. Vegetation of La Michilía is dominated by oak-pine forests (*Quercus* spp., *Pinus* spp., *Juniperus* sp., *Arctostaphylos pungens*). The Bolsón de Mapimí is a basin crossed by small mountains within the playas of the alluvial plains (elevation 1000–1350 m). The climate is arid with summer rains and cool winters. The average annual precipitation is 264 mm. The annual mean temperature varies between 3.9°C and 33°C. The Mapimí reserve contains a xerofitic shrubland vegetation (*Larrea divaricata, Fouquieria splendes, Prosopis glandulosa, Opuntia* spp., and *Hilaria mutica*).

La Michilía was surveyed in early September 1981 and late March 1982. Mapimí was surveyed from late March through early September in 1985 and 1986. As I was not able to distinguish between residents and migrants, and knowing that foraging flight may differ between the two groups, I did not make observations during the months when migrants could be in the area. Observations of foraging groups were made opportunistically from a car and from elevated vantage points between 09:30 and 16:00 h in both areas. Following Rabenold (1983) and Prior (1990), birds were considered to be in the same foraging group whenever they were observed in the air within 1 km of one another and heading in the same direction. For every foraging individual and group, I recorded the time of day, altitude of flight, and type of flight (flapping or soaring). I used a clinometer on several objects of known altitude and distance to confirm the accuracy of the estimations. I analyzed group size and flight altitude differences using chi-square tests. These tests detected differences between the two study areas in the frequency of four size groups, at three heights (below

TABLE 1

FORAGING GROUP SIZE OF TURKEY VULTURES IN THE FOREST OF LA MICHILÍA AND THE DESERT OF MAPIMÍ, DGO., MÉXICO

	La Michilía		Mapimí	
Group size	N	%	N	%
1	75	68.2	57	57.0
2	22	20.0	23	23.0
3	9	8.2	4	4.0
4	1	0.9	8	8.0
5	1	0.9	2	2.0
6	1	0.9	3	3.0
7	1	0.9	2	2.0
8	—	—	1	1.0
Mean group size	1.53		1.97	

50 m, between 50–100 m or above 100 m), and at three times of day. Differences in the mean group size (MGS) were analyzed using Kolmogorov-Smirnov two sample tests.

Results.—Turkey Vultures in La Michilía and Mapimí foraged solitarily in 68% and 57% of my observations, respectively (Table 1). The occurrence of groups was similar in both regions, except that groups of more than three individuals were significantly more frequent at Mapimí ($\chi^2 = 9.4$; df = 1; $P < 0.01$; Table 1). Differences were not found between the MGS of La Michilía and Mapimí (Kolmogorov-Smirnov, two sample test; $P > 0.05$). Dividing hourly observations into three periods (before 11:00, 11:00 to 14:00, and after 14:00) showed significant differences in group size with the time of day ($\chi^2 = 11.2$; df = 2; $P < 0.01$). Group size was higher between 11:00 and 14:00 in both La Michilía and Mapimí, although in Mapimí, Turkey Vultures began to fly earlier.

TABLE 2

COMPARISON OF FLIGHT ALTITUDE OF TURKEY VULTURES DURING FORAGING ACTIVITIES AT LA MICHILÍA AND MAPIMÍ, DURANGO, MÉXICO

	Group size			
Flight altitude (m)	1	2	3	>3
0–50				
Michilía	41	8	1	0
Mapimí	39	13	3	10
50–100				
Michilía	24	3	3	1
Mapimí	18	7	1	3
>100				
Michilía	10	11	5	3
Mapimí	—	3	—	3

Turkey Vultures most often flew within 50 m of ground level in both La Michilía and Mapimí (Table 2). However, at La Michilía Turkey Vultures flew more often at altitudes above 100 m than they did at Mapimí ($\chi^2 = 15.6$; df = 1; $P < 0.01$; Table 2). Turkey Vultures foraged at Mapimí in groups larger than three individuals only at altitudes below 50 m, while at La Michilía groups of more than three individuals were observed at altitudes higher than 100 m.

Discussion.—Turkey Vultures in the forest of La Michilía and in the desert of Mapimí generally foraged at altitudes below 50 m, as reported by other authors for different habitats (Stager 1964, Coleman and Fraser 1987, Houston 1988). As has been observed in other regions (Stewart 1978, Rabenold 1983, Prior 1990), most of the time Turkey Vultures at La Michilía and Mapimí search solitarily or in pairs. However, in other forests of North America, they forage in larger groups than they do in La Michilía. Differences were noted between the MGS reported in other North American populations and those of northern Mexico (MGS 2.31, North Carolina: Prior 1990; 2.75, North Carolina: Rabenold 1983; 1.53, La Michilía: this study) ($P < 0.001$, Kolmogorov-Smirnov two sample tests). However, the mean group size reported in a forest in Southern Ontario (MGS 2.11: Prior 1990) is similar to that recorded in the La Michilía forest ($P > 0.05$, Kolmogorov-Smirnov, two sample test). Prior (1990) suggests that lower population densities of Turkey Vultures may be responsible for the small size of foraging groups. The density of Turkey Vultures in La Michilía has been estimated at 0.75 birds/km (Hiraldo et al. 1991) and in Mapimí at 0.53 birds/km (Rodríguez-Estrella, unpubl. data). These figures indicate a low population density in both regions, and the MGS of these two southern regions is similar to that of Ontario's Turkey Vulture population.

Factors other than population density could be responsible for foraging group size. Group size in Mapimí was not significantly larger than that in La Michilía, but Turkey Vultures in Mapimí flew at lower altitudes than those in La Michilía. The higher density and cover of the La Michilía vegetation does not seem to be an important factor since Turkey Vultures locate carrion mainly by smell (Bang 1964, Houston 1986). Probably the size of potential carcasses and their scarcity may explain this. The feeding habits of Turkey Vultures in both regions support this idea, since small and medium-sized prey comprised 78% of the items in the Mapimí diet (Rodríguez-Estrella 1993), whereas in La Michilía, they comprised 42% (Hiraldo et al. 1991). Also, the density of large mammals in Mapimí (i.e., Mule deer [*Odocoileus hemionus*]) seems to be lower than in La Michilía (i.e., White-tailed deer [*O. virginianus*]) (Ezcurra and Gallina 1981). Although Turkey Vultures consume smaller prey in areas where it coexists with the Black Vulture (Stewart 1978, Coleman and Fraser 1987, Hiraldo et al. 1991), the difference in the diets between Mapimí and Michilía, where Black Vultures are absent, probably reflects the availability of the prey sizes in both areas, particularly of the wild and domestic ungulates. On the other hand, Houston (1974) found that African vultures search for large carcasses at higher altitudes because they are able to cover a wider area in this way. Thus, Turkey Vultures may search in larger groups at higher altitudes in the forest of La Michilía because more profitable larger carcasses are available than in the desert of Mapimí, where a low flight is the most efficient method for finding small and medium carcasses.

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Nest-site characteristics of four raptor species in the Argentinian Patagonia.—The selection of an appropriate nest site is vital to the reproduction of birds because it determines the environment to which adults, eggs, and altricial chicks will be exposed during critical periods. In general, both nest-site selection and construction should provide the necessary protection against predation of eggs and nestlings. The environmental conditions in the nest will be affected by the nest architecture, its exposure to the winds, protection from storms, and insolation.

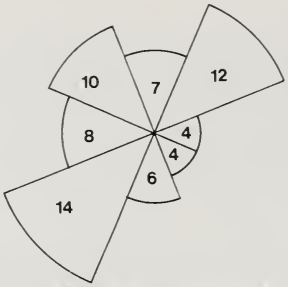
The objective of this study was to describe the nest and nest-site characteristics of four diurnal raptor species of the Argentinian Patagonia. There were the Grey Eagle-Buzzard (*Geranoaetus melanoleucus*), Chimango Caracara (*Milvago chimango*), Crested Caracara (*Polyborus plancus*), and Red-backed Hawk (*Buteo polyosoma*). Information on nest-site characteristics of these species is scarce over their entire geographical range (see Brown and Amadon 1968, Fraga and Salvador 1986, Jiménez and Jaksic 1990) with the exception of the Crested Caracara in North America (Palmer 1988).

Methods.—We collected data for this study in the Neuquén province, northern Argentinian Patagonia, in a circle of 60 to 70 km radius centered at the city of Junín de los Andes (39°57′S and 71°05′W), 780 m above sea level. The area belongs to the Patagonian Phytogeographic Province, Occidental District (Cabrera 1976). The vegetation is characterized by a mixed steppe of grass and shrubs. Dominant grass species are *Mullinum spinosum, Senecio* spp., *Stipa* spp., and *Poa* spp., while common shrubs are *Chacaya trinervis, Berberis darwinii,* and *Schinus molle.* Dominant trees are *Austrocedrus chilensis, Nothofagus* spp., and *Araucaria araucana.* The habitats present are great plains of 800–900 m high, dissected by steep rugged areas and valleys of different sizes. In the bottom of these valleys there are humid areas with dense herbaceous vegetation ("mallines") where dominant species are *Cortadeira araucana, Juncus* sp. and *Carex* sp. Arboreal species such as *Maytenus boaria* and *Salix humboldtiana* are concentrated in valleys and mallines. Pine plantations (*Pinus* spp.) are also present in the study area.

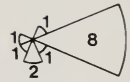
The weather is dry and cold, with frosts throughout almost all the year, and frequent winter snowfalls. Mean, mean highest, and lowest annual temperatures are 11, 17.4, and 2.5°C, respectively. Absolute maximum temperatures for the spring season (September–December) ranges from 30°C in September to 37°C in December, while absolute minimum temperatures were −12.3°C and −3.5°C for the same months, respectively. Annual rainfall is 600 mm, with 20% in spring. Solar radiation increases from 300 cal/cm^2 day in September to 540 cal/cm^2 day in December. Spring mean cloud cover is about 4.1 (measured in a 1–8 scale). The most important weather feature in Patagonia is strong cold winds which can reach a speed of up to 120 km/h. During spring, they blow from the Andean range, in an easterly direction, towards the Patagonian steppe (Fig. 1).

Nests were located by (1) personal inquiries to land owners and their employees, (2) vehicle trips along main and secondary roads, and (3) cross-country foot trips. We used binoculars (10 × 40) and telescopes (field scopes) (20× to 40×) to check hills, cliffs, trees, and any other potential nesting sites, and we frequently located nests by observing the adult birds.

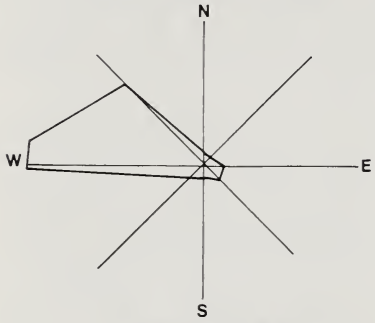
Once the nest had been spotted and its occupant-species identified, its location was plotted on a map (topographic sheets of Argentinian Army Geographic Institute, scale 1:50,000 and 1:100,000). The nests were classified as active (with eggs or young) or inactive (repaired or in good condition). We discarded from the analyses those nests showing deterioration or any other sign of having been unoccupied the previous breeding seasons. For each nest, a field data sheet was completed with the following information (variables were based on the



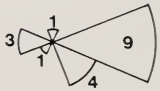
GREY EAGLE-BUZZARD



CHIMANGO CARACARA



WIND DIRECTION



CRESTED CARACARA

FIG. 1. Incoming wind direction and nest orientation of Grey Eagle-Buzzard, Chimango Caracara, and Crested Caracara nests in the Argentinian Patagonia. Values are total nests which are exposed in each sector.

features that were listed in previous literature as important or relevant to descriptions of nest sites) (1) substrate height: distance in meters from the base to the top (shrubs, trees and cliffs) of the substrate, (2) nest height: distance in meters from the substrate base to the nest, and (3) nest-site orientation: in the case of nests located in trees or shrubs, measured as the deviation from the north around the central vertical axis of the trunk. In the case of nests on cliffs, nest-site orientation was measured as the deviation from the north (1) of the cliff face where the nest was placed, or (2) of the nest when its orientation did not coincide with that of the cliff. Measurements were then grouped in 45° octants corresponding to orientations N, NE, E, SE, S, SW, W, NW.

Results and discussion.—Nest orientation was examined using chi-square for Grey Eagle-Buzzards and Rayleigh's test (Zar 1974) for the Chimango Caracaras and the Crested Caracaras because of insufficient data to perform a chi-square test. Critical values were selected at the 0.05 probability level for tests of significance. A total of 162 nests were located: 101 of Grey Eagle-Buzzards, 33 of Chimango Caracaras, 19 of Crested Caracaras, and 12 of Red-backed Hawks. Chimango Caracaras used a wide range of nesting substrates (trees, shrubs, cliffs, ground, and poles); a wide range was also observed for the Grey Eagle-Buzzard (trees, cliffs, and power-poles), while Crested Caracaras and Red-backed Hawks always nested in trees and shrubs (Table 1).

Grey Eagle-Buzzard nests were at midheight when they were in cliffs but tended to

TABLE 1

NEST-SITE CHARACTERISTICS OF FOUR PATAGONIAN RAPTORS

Species	Substrate	Substrate height (m)	Nest height (m)	Relative nest position relative to substrate height (%)
Geranoaetus melanoleucus[a]	Trees (8)			
	Populus tremuloides	22.5 (2)	14.0	61.0
	Austrocedrus chilensis	11.5 (2)	11.0	96.0
	Maytenus boaria	8.0 (2)	5.5	69.0
	Chacaya trinervis	5.0 (1)	5.0	100.0
	Cliffs (92)	19.34 ± 9.6 (90)	12.69 ± 8.2	64 ± 18.1
Milvago chimango[b]	*Chacaya trinervis* (3)	4.0 (3)	2.4	50.0
	Berberis darwinii (17)	2.3 ± 0.8 (17)	1.7 ± 0.4	74 ± 14.8
	Scirpus californicus (4)		0.6 ± 0.4	
Buteo polyosoma	*Schinus molle* (6)	2.4 ± 0.5 (5)	2.2 ± 0.4	92 ± 14
	Chacaya trinervis (5)	3.8 ± 0.9 (4)	30 ± 0.9	80 ± 9.0
	Salix humboldtiana (1)	4.0 (1)	3.0	75.0
Polyborus plancus	*Populus tremuloides* (14)	19.9 ± 7.8 (13)	8.0 ± 3.61	43 ± 14.5
	Maytenus boaria (1)	6.0 (1)	4.5	76.0
	Araucaria araucana (1)	13 (1)	9.0	70.0
	Berberis darwinii (1)	4.0 (1)		
	Salix humboldtiana (1)	8.0 (1)	4.0	50.0
	Nothofagus spp. (1)	5.0 (1)	5.0	100.0

[a] One nest in a power pole, not considered for calculations.
[b] Six nests on the ground and three on cliffs, not considered for calculations.

occupy the most distant extreme when they were on trees, apparently limited only by branch strength. Chimango Caracaras showed a strong tendency to place their nests in or near the central place of the substrate (Table 1). Crested Caracaras tended to occupy the lower half portion of the tree when nesting on aspens (*Populus tremuloides*), an introduced tree. The Red-backed Hawk tended to occupy distal extremes of shrubs and trees (Table 1).

Grey Eagle-Buzzard, Chimango Caracara, and Crested Caracara oriented their nests (Fig. 1), while Red-backed Buzzard showed no clear orientation, nesting in all occasions on the tops of trees and shrubs (N = 12). Compass orientation of Grey Eagle-Buzzard nests on cliffs did not differ from a random distribution ($\chi^2 = 5.54$, df = 7, $P = 0.59$), but all four tree nests were oriented to the east. Chimango Caracaras and Crested Caracaras also showed a strong tendency to orient their nest eastwards (Rayleigh's test $R = 0.58$, $P < 0.05$ and $R = 0.47$, $P < 0.05$, respectively).

Grey Eagle-Buzzards prefer to nest on trees or cliffs, depending on local substrate availability (Jiménez and Jaksic 1990). The only published descriptions of Chimango Caracara nests refer to ground nests and those of a small colony in trees (Fraga and Salvador 1986), although this species nests on a variety of substrates in Argentina. Crested Caracaras nest in shrubs and trees, including lateral branches of giant cactus in North America (Palmer 1988). Finally, information on nest-site characteristics for the Red-backed Hawk was also scarce. When trees or bushes are available it nests in them, but a ledge, telephone pole, or rock were also used as a nest-site (Brown and Amadon 1968).

Nests of large raptors can be destroyed by carnivores and humans; when predation risk is absent, large eagles may nest on the ground (Newton 1979). In our case, Grey-Eagle Buzzards seem to nest in places where the risk of mammalian predation is low (middle place on cliffs, distal extreme on trees) as do other large eagles worldwide (Newton 1979, Gargett 1991, Ferrer 1993). The Chimango Caracara, the smallest raptor considered in our study, decreases predation risk by nesting in unaccessible places such as the center of spiny shrubs and leafy tree areas. It frequently covers the upper portion of the nest with small branches and spiny leaves similar to a domed nest (Collias and Collias 1984).

Trees and shrub nests of Crested Caracaras, Chimango Caracaras and Grey Eagle-Buzzards were oriented eastward, the most protected direction from the cold westerly winds (Fig. 1). Nevertheless, when observing Grey Eagle-Buzzard nests on cliffs, we found no predominant orientation. This failure in detecting a clear orientation could be a consequence of the high density reached by this species in the study area (Travaini et al. 1992). Any possible selection could be obscured by habitat saturation that would restrict possible nest orientations for many pairs. In the Red-backed Hawk, the selection of tree and shrub tops where it nests, together with the lack of an orientation direction in its nest-sites, may be compensated for by nesting in trees or shrubs located in wind-protected, small- or medium-sized valleys (11 of the 12 nests in this study were in narrow valleys).

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Notes on egg laying and incubation in the Common Merganser.—Common Mergansers (*Mergus merganser*) are large, piscivorous, cavity-nesting ducks with a broad distribution in North America (Bellrose 1980). Their foraging habits (i.e., reliance on fish) and the sensitivity of their breeding habitat in eastern North America make them an ideal indicator species for studying the effects of environmental pollution on aquatic food webs (Haseltine et al. 1981, McNicol et al. 1990), but little is known about their nesting biology (Bellrose 1980, Afton and Paulus 1992). Here we describe egg laying, clutch size, incubation behavior, and mass loss of female Common Mergansers nesting in nest boxes in the Temagami region (47°N, 80°W) of northeastern Ontario, Canada.

Patterns of nest attentiveness and mass loss were recorded using load cell monitoring systems installed in nest boxes during egglaying (method described in Mallory and Weatherhead 1992). A "recess" was a period of time the female spent off the nest, and "nest attentiveness" was the amount of time the female spent on the nest each day, expressed as a percentage of 24 hr (Afton and Paulus 1992). Because these monitors recorded on strip charts, movements by the female while incubating are recorded as a spike along a continuous line. Thus while we were able to document the frequency of female movements during incubation, we were not able to distinguish between egg turning and comfort movements.

Clutch size was the maximum number of Common Merganser eggs in the nest box prior to incubation. We also recorded instances of nest parasitism by other cavity-nesting ducks. Nest box use by all species is described in Mallory et al. (1993).

Ten Common Mergansers used our nest boxes between 1975 and 1984. Mean clutch size was 9.1 ± 0.8 eggs (N = 10). Two nests were parasitized each by Common Goldeneyes (*Bucephala clangula*) and Hooded Mergansers (*Lophodytes cucullatus*), while Common Mergansers parasitized two nests of other species. In 1981, we installed three monitors in Common Merganser nests prior to clutch completion. We recorded eight egg-laying times for three females. The females spent an average of 373 ± 48 min (±SE, N = 6) on the nest as each egg was laid. However, on two other occasions, females laid eggs late in the afternoon and remained on the nest overnight (910 ± 26 min). Using the start of each egg-laying session as the egg-laying time, the mean interval between eggs was 1.3 ± 0.2 days (N = 7).

We defined the first day of incubation as the day following the first night that the female remained on the nest following clutch completion. One of the three females deserted her nest after this first night of incubation. The other females began incubation on 6 May and 19 May. Incubation was not always recorded on consecutive days but covered most of the incubation period (day one to 26). Twelve and seven days of incubation were recorded for these two females, respectively, and mean values were used for incubation days on which both females were recorded, yielding fifteen days of pooled incubation data. The females departed their nests at 09:31 ± 24 min for their morning (first) recess (N = 15 for all comparisons unless otherwise noted) and returned from their last recess at 18:45 ± 18 min to begin continuous night incubation. One recess was usually taken in the morning, while one or two shorter recesses where taken in the afternoon. Females spent 165 ± 12 min off the nest each day; consequently nest attentiveness averaged 88.5 ± 0.9%. Females took 1.9 ± 0.1 recesses each day, for an average duration of 88.4 ± 10.7 min (N = 24). Nest attentiveness declined as incubation proceeded ($r = -0.58$, N = 15, $P = 0.02$). Females adjusted nest attentiveness by varying the duration of recesses ($r = -0.66$, $P = 0.007$); the number of daily recesses was not correlated significantly with nest attentiveness ($r = 0.13$, $P = 0.6$). When females took longer recesses, they decreased the number of trips off the nest ($r = -0.79$, $P = 0.001$).

While on the nest, females adjusted their position on the eggs approximately three times each hour, but the frequency of movements differed according to the time of day. During morning incubation (after returning from the first recess), females moved in the nest every 18.2 ± 0.3 min (N = 213), while during the afternoon they moved at 26.2 ± 0.5 min intervals (N = 297) and at night they moved at 26.7 ± 0.4 min intervals (N = 322). These values differ significantly (ANOVA, $F = 106$, df = 1,829, $P < 0.001$), with morning intervals shorter than afternoon and evening intervals (Newman-Keuls test, $P < 0.05$).

One female began incubation weighing 1105 g and had lost 90 g (8.1% of her initial mass) seven days later. The other female began incubation weighing 1300 g and lost 175 g (13.5%) over 25 days. If mass loss continued at the same rate (0.87%/day) through incubation, we estimate that these females lost about 27% body mass while incubating (using mass loss equation in Afton and Paulus 1992).

Our measures of clutch size and female mass are similar to values reported previously (Bellrose 1980, Eriksson and Nittyla 1985). Moreover, our estimates of nest attentiveness and mass loss of incubating Common Mergansers are consistent with results for other members of the Tribe Mergini (see Afton and Paulus 1992) and with the general pattern among waterfowl that larger species have higher nest attentiveness (Afton and Paulus 1992). Also, Common Mergansers incubated continuously during the night, typical of other cavity-nesting waterfowl (e.g., Afton and Paulus 1992, Mallory et al. 1993). Finally, Common Mergansers

turned their eggs at approximately the same rate as the similarly-sized Mallard (*Anas platyrhynchos*) (Caldwell and Cornwell 1975). Thus, the nesting behavior of this species appears to conform to the general patterns established for waterfowl (Afton and Paulus 1992).

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Sleeping and vigilance in the White-faced Whistling-Duck.—Several hypotheses have been proposed to explain the function of sleep in birds (Amlaner and Ball 1983). Of particular interest is the trade-off between anti-predator vigilance and sleep. Short periods of eye opening, referred to as "peeks" (Lendrem 1983), regularly interrupt sleep in several species of birds. Birds have elevated arousal thresholds when peeking (Amlaner and McFarland 1981) and are able to move quickly if threatened by a predator (Lendrem 1983, 1984). Peeking behavior, therefore, has been considered to be an analogue to scanning behavior in active birds (Lendrem 1983). Like scanning, peeking has been reported to decrease with increasing group size of sleeping birds (Lendrem 1984). However, detailed field studies of sleeping-vigilance trade-off in birds are scarce. In this paper, we consider the effect of position in the group and time of day on vigilance during sleeping in the White-faced Whistling-Duck (*Dendrocygna viduata*).

The White-faced Whistling-Duck is a medium-sized duck found in West Africa and South America. Its feeding ecology and behavior were described by Roux et al. (1976), Douthwaite (1977) and Clark (1978). During the day, White-faced Whistling-Ducks devote most of their time to sleep, vigilance and comfort activities (Roux et al. 1976). Compared to other duck species wintering in West Africa, they appear to be particularly sensitive to disturbance by potential predators (Roux et al. 1978). Data were collected from 8:00 h to 17:00 h (local time) on two consecutive days of intensive observation at Goram in the Djoudj National Park, Senegal, West Africa, in April 1993. Vigilance rates were recorded for randomly selected individuals sleeping in a flock ranging from 300 to 496 (mean group size = 481). Sleeping birds that were floating on the water were observed with a 20× telescope. Two sleeping postures (Amlaner and Ball 1983) were used by White-faced Whistling-Ducks. In the sleep posture, the bill was pointed backwards under the scapulars. In the rest-sleep posture, the bird was floating with its head up and bill pointing forward. Focal birds were randomly selected. The observer (M.G.-C.) in a blind attempted to follow a focal bird for one minute, recording on a tape recorder the time of day, flock size, number of peeks, sleeping posture and position of the bird in the group. Males and females are alike and therefore were not distinguished in the wild. Ducks were considered central if they were part of the central 80% of the aggregation. Recording was sometimes interrupted when the bird awoke before the completion of the observation. We ran stepwise multiple regression analyses (Sokal and Rohlf 1981) to regress peeking rates (number of peeks per minute) on first to fourth degree terms of flock size and time of the day. A "predictor" equation was obtained by entering variables into the regression equation according to their F-to-enter values, provided they explained a significant portion of the observed variance in the dependent variable (peeking rate). We used an F statistic and a criterion of $P < 0.05$ in assessing the contribution of each independent variable to the total variance. The residuals of the multiple regression were used to study the effect of sleeping posture and position in the group on vigilance, using two-way ANOVAS (Sokal and Rohlf 1981).

The data set consisted of 72 focal observations. There was no relationship between peeking rate and the duration of a focal observation, i.e., observation time did not bias the results. Peeking rates of White-faced Whistling-Ducks were normally distributed (mean peeking rate: 18.4 ± 8.1 peeks/min). Peeking rates in White-faced Whistling-Ducks varied significantly according to time of day (Fig. 1). Only the linear term of time of day was retained in the multiple regression. There was no detectable effect of group size on peeking rates in the range of observed flock sizes. Sleeping posture did not influence peeking rate ($F_{1,68} = 0.516$, $P > 0.05$) nor did position within the group ($F_{1,68} = 0.072$, $P > 0.05$).

The observed high susceptibility of White-faced Whistling-Ducks towards predator disturbance (Roux et al. 1978) is here confirmed by the elevated peeking rates, compared to other duck species (Lendrem 1983; Cézilly et al., unpubl. data). The absence of a significant effect of group size on peeking rates may be due to the limited amount of variation in flock size within this study. Only large groups of White-faced Whistling-Ducks were observed, and it is likely that the decrease in vigilance levels between group sizes of 300 and 400 would be quite small, if any exists.

Time of day can influence vigilance in several ways. Lima (1988) showed that vigilance in Dark-eyed Juncos (*Junco hyemalis*) is high in the early morning because of the increased risk of predation when foraging in dim light. McNamara and Houston (1986) have suggested that vigilance rates may vary according to the time of day in relation to energetic requirements. Temperature is likely to correlate with time of the day, and variation in temperature has been shown to affect the use of sleeping postures in Black-billed Magpies (*Pica pica,* Reebs 1986). However, daily temperature showed little variation at the time of data collection in the present study. White-faced Whistling-Ducks forage mainly two hours after dawn

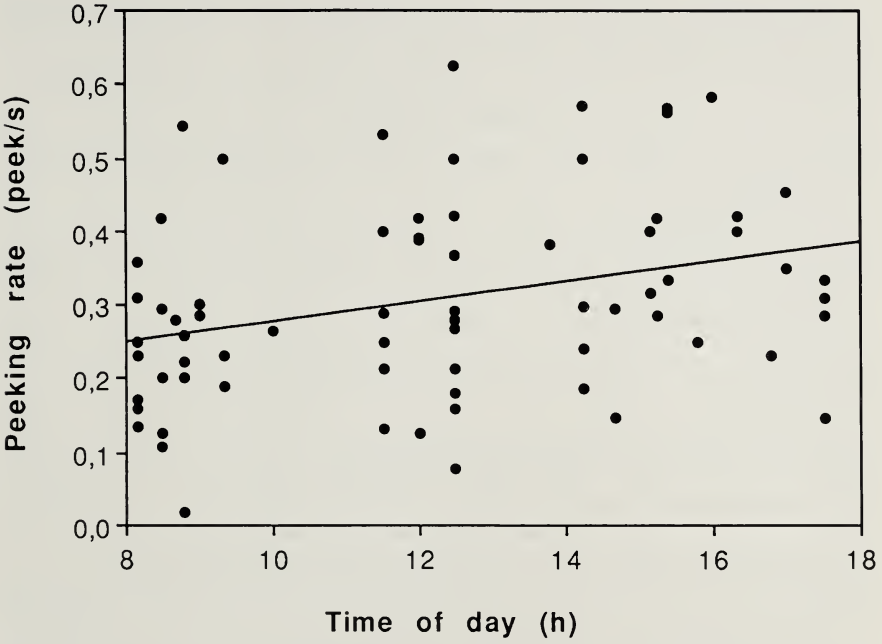

FIG. 1. Variation in the peeking rate of White-faced Whistling-Ducks according to time of day ($r = 0.31$, N = 72, $P < 0.05$).

and before dusk (Brown et al. 1982). The observed slight, yet significant, increase in peeking rate from early morning to late afternoon might therefore reflect a progress in the level of arousal between two peaks of activity.

Various postures can be used by birds while sleeping (Amlaner and Ball 1983). It is however not clear whether different postures represent different arousal thresholds (Amlaner and McFarland 1981). Observations of Herring Gulls (*Larus argentatus*) (Amlaner and McFarland 1981) showed that peeking was less frequent during the sleep posture than during the rest-sleep posture. This was not the case in the White-faced Whistling-Ducks where the two postures appeared to be used equally. Among 72 randomly selected individuals 32 birds were in the sleep posture and 40 in the rest-sleep posture (binomial test, $z = 0.83$, $P = 0.203$).

Birds on peripheries of foraging flocks have been previously shown to spend more time scanning the environment as compared to other group members (Jennings and Evans 1980, Inglis and Lazarus 1981, Petit and Bildstein 1987). This was not the case in White-faced Whistling-Ducks. Westcott and Cockburn (1988) also found that position in the flock did not influence scanning rate or total time spent scanning in the Red-rumped Parrot (*Psephotus haematonotus*). They interpreted this result in relation to foraging constraints and the need to monitor the behavior of conspecifics. In the case of the White-faced Whistling-Duck, the absence of edge effect may be explained in relation to the type of predator attack. Individuals in the periphery of flocks would be particularly exposed to predation in the case of a ground predator. In the case of an aerial predator, however, it is less clear that birds in the center of flocks would experience higher safety.

Sleeping-vigilance trade-off in birds is likely to be affected by a variety of environmental and social factors (Elgar 1989). The present study suggests that its relationship with other components of circadian activity deserves further attention.

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Drinking methods in two species of bustards.—Most birds drink water by scooping it up with their beaks and tilting their head backwards, allowing the water to run down their throat. There are a few families of birds, however, such as the Columbidae (Wickler 1961), Estrildidae (Poulsen 1953), Spermestidae (Immelmann 1962), Coliidae (Cade and Greenwald 1966), Turnicidae (Fry 1978), and Otididae (Fisher et al. 1972) in which all or some of the species drink water using a sucking method. Suction drinking is believed to be an adaptation for obtaining water in arid climates. It is believed that by using this method the bird is able to utilize small amounts of water efficiently and quickly (Immelmann 1962). Since it is a rather quick method, Cade (1965) and Immelmann (1962) have suggested that it may be advantageous to the bird by reducing the amount of time at the water source, and hence, the likelihood of being attacked by predators. In this method, the beak is immersed in water, and the bird draws in water by pumping of the throat. There are also some species that employ a third and intermediate method of drinking, whereby water is sucked into the mouth using the same sucking action as described as above, followed by raising of the head in order to swallow. Members of the family Pteroclidae (Cade et al. 1966) and Dicruridae (Skead 1975) are reported to use this method. Two species of bustards, the Kori Bustard (*Ardeotis kori*), and the Buff-crested Bustard (*Lophotis ruficrista*) were observed drinking water and their drinking methods are reported in this paper.

At the National Zoological Park, where Kori Bustards are exhibited, drinking was observed on numerous occasions. Water is available at all times, and the birds were observed drinking water throughout the year. It is not unusual for a bird to drink for over two min at interrupted intervals. One position assumed by the birds when they drink is identical to that described by Fisher et al. (1972) for the Australian bustard, and by Ali and Rahmani (1981–1982) for the Great Indian Bustard (*Ardeotis nigriceps*). In this position, the bird sits down while drinking. Fisher et al. stated that the only other bird that sits in this position to drink is the Emu (*Dromiceius novaehollandiae*). Another common position observed is that the birds simply remain standing to drink. In both positions, it is clear that the birds were using a sucking action to obtain the water.

In the Buff-crested Bustard, drinking was observed on one occasion by a pair housed at the Baltimore Zoo. A video camera was used to observe the birds' drinking methods. In this species, an intermediate form of drinking was used, and the bird remained standing for the several bouts of drinking observed. It was the same method described by Skead for the Forktailed Drongo (*Dicrurus adsimilis*) where a sucking action was used to draw the water in, after which the head was tilted back to allow the water to run down the throat.

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Brown-headed Cowbirds fledged from Barn Swallow and American Robin nests.— Brown-headed Cowbirds (*Molothrus ater*) have parasitized at least 220 species of birds, of which approximately 144 species have raised cowbird young (Friedmann and Kiff 1985, Lowther 1993). For several species, records of parasitism are rare or based on circumstantial evidence. Here I document two unlikely species, American Robin (*Turdus migratorius*) and Barn Swallow (*Hirundo rustica*), raising Brown-headed Cowbirds at least to fledging age.

There is only one reported case of Barn Swallows raising a young cowbird (Sutton 1967), but it was undetermined if the cowbird fledged. Other accounts of Barn Swallows being parasitized are rare. No parasitism was observed in 322 Barn Swallow nests found between 1963 and 1975 in Louisiana (Goertz 1977), nor 185 nests in Iowa (Lowther 1985, 1991), and Hill (1976) found no parasitism in 284 nests in Kansas. Friedmann (1929) cites a single report in Iowa with little detail. More recently, Friedmann (1963, 1971; Friedmann et al. 1977), in addition to citing the Oklahoma record, mentions three records of parasitized Barn Swallow nests from Pennsylvania, one from Maryland, one from Manitoba, two (0.1%) of 1977 from Ontario, "several" from Kansas, and none out of 3776 nest records in the Cornell Univ. files.

Out of 67 Barn Swallow nesting attempts I observed in Osage County, Oklahoma, two (same nest twice) were parasitized by cowbirds. The first nest, first active on 30 May 1992, contained one cowbird egg and five Barn Swallow eggs. The nest was checked twice weekly until all young fledged. By 19 June, the cowbird egg had hatched and the nestling was two or three days old. On 23 June, the Barn Swallow eggs had recently hatched. The cowbird chick was banded on 26 June and was very near fledging. On 30 June the cowbird chick was gone and four swallow chicks remained. The last Barn Swallow chick fledged on 14 July, at least 14 days after the cowbird had left the nest. The cowbird was never seen outside of the nest, so it is not known whether it survived to independence. In the second parasitized swallow nest (late July) the cowbird egg failed to hatch.

The American Robin is known to be a rejecter of cowbird eggs (e.g., Friedmann 1929, Rothstein 1975). However, Brown-headed Cowbird eggs occasionally appear in robin nests.

Reported cases include one (0.8%) of 120 nests at Buckeye Lake, Ohio (Trautman 1940), one (0.2%) of 486 nests in British Columbia (Friedmann 1963), nine (0.3%) of 3586 nests in Ontario (Friedmann 1977), one (0.5%) of 216 nests in Louisiana (Goertz 1977), and one (0.5%) of 205 nests from Iowa (Lowther 1985). However, Elliott (1978) found two (40.0%) of five robin nests parasitized in Kansas. None of the parasitized robin nests reported above were known to have raised cowbird young.

Documented cases of cowbirds being reared by robins are very scarce. Trautman (1940) mentioned three cases of cowbird fledglings being fed by robins, but provided no details. Hodges (1949) located a robin nest in Iowa containing a cowbird nestling close to fledging, the first real evidence that robins may occasionally raise cowbirds. Lowther (1981) observed a fledgling cowbird being fed by an adult robin for 11 days in Kansas, but it is uncertain if the cowbird had been raised by the robin or had been adopted.

During 1992–1993 I found two (4.3%) of 47 robin nests parasitized in Osage County, Oklahoma. The first nest was found while under construction on 30 April 1993. On 4 May, it contained four robin eggs, and one cowbird egg. By 7 May, the nest was again empty, most likely depredated. The second nest also was found while under construction on 13 May 1993, and was empty on 17 May. On 20 May, the nest contained three robin eggs and one cowbird egg, all being incubated by the female robin. On 1 and 3 June the nest contained a cowbird nestling, one robin nestling, and two robin eggs. By 7 June the cowbird was close to fledging, and on 10 June only the robin chick and one robin egg were in the nest. The remaining egg and the interior of the nest were covered with feces, indicating that the cowbird nestling probably fledged. By 14 June the robin chick had also fledged. The robins and fledgling cowbird were not seen again.

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Lead poisoning in a Mississippi Sandhill Crane.—Lead poisoning from the ingestion of spent lead shot is well documented in waterfowl (Sanderson and Bellrose 1986) and has been reported in other wetland (Locke et al. 1991, Windingstad et al. 1984) and upland (Hunter and Rosen 1965, Locke and Bagley 1967) avian species. Ingested fishing weights have been implicated in lead poisoning of Trumpeter Swans (*Cygnus buccinator*) (Blus et al. 1989), Common Loons (*Gavia immer*) (Locke et al. 1982, Franson and Cliplef 1992, Pokras and Chafel 1992), Mute Swans (*Cygnus olor*) (Birkhead 1982), and Sandhill Cranes (*Grus canadensis*) (Windingstad et al. 1984). The significance of lead poisoning as a mortality factor in avian species other than waterfowl is probably underestimated (Locke and Friend 1992), and any cause of mortality becomes particularly important in species with small population sizes. We report here the first known case of lead poisoning in a Mississippi Sandhill Crane (*Grus canadensis pulla*), a critically endangered subspecies.

The Mississippi Sandhill Crane exists in the wild only in Jackson County, Mississippi, on the Mississippi Sandhill Crane National Wildlife Refuge (refuge) and adjacent private lands. In 1981, a program was initiated to supplement the free-ranging population by releasing Mississippi Sandhill Cranes on the refuge that were hatched and raised at the Patuxent Wildlife Research Center (Zwank and Derrickson 1981). As of 1 October 1993, 207 captive-reared cranes had been released, and the total wild population was 130 birds. One of the captive-reared cranes was found dead on the refuge on 27 February 1992, about 10 weeks after its release. Necropsy examination at the National Wildlife Health Research Center revealed the carcass to be that of a juvenile female weighing 2940 g. It was in poor flesh with an absence of fat reserves and markedly reduced pectoral musculature. No lesions of infectious disease or trauma were noted. The gall bladder was 2 cm in diameter by 4 cm in length and contained dark green bile. No food was present in the esophagus, proventriculus, or gizzard. The gizzard lining was dark brown and roughened, and within its contents were several small stones and a soft gray metal object. The object was triangular ($8 \times 8 \times 10$ mm), nearly flat, and easily deformed by pressure with a sharp instrument (Fig. 1).

Tissues were collected from the crane for laboratory testing using standard techniques in histopathology, microbiology, virology, and parasitology. Duplicate liver samples were homogenized, dried, and ashed in preparation for lead analysis by atomic absorption spectrophotometry according to Locke et al. (1991). The mean recovery rate for standard

FIG. 1. Soft metallic object found in the gizzard of a Mississippi Sandhill Crane (*Grus canadensis pulla*) that died of lead poisoning. Marks in the upper left quadrant were made by pressure with a pair of shears.

samples spiked with lead was 95%. Liver lead concentrations were 69 and 70 ppm wet weight, well above the 8 ppm wet weight considered consistent with lead intoxication in waterfowl (Friend 1985) and higher than levels previously reported in two lead poisoned Sandhill Cranes (Windingstad et al. 1984). Microscopic examination of tissues revealed hemosiderosis, accumulation of iron-containing pigment, in the liver and spleen. Although not specific for lead poisoning, this finding is consistent with observations in lead poisoned waterfowl (Wobeser 1981). Results of microbiology, parasitology, and virology were negative. A diagnosis of lead poisoning was issued based on gross and microscopic findings, the presence of the metallic object in the gizzard contents, and the high liver lead concentration.

Avian mortality from an acute exposure to metallic lead usually occurs well before 10 weeks have elapsed (Friend 1985, Franson et al. 1986, Pattee et al. 1981, Windingstad et al. 1984). Therefore, we conclude that the Mississippi Sandhill Crane ingested the metallic object, the source and identity of which remain unknown, after its release on the refuge.

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Maroon-bellied Conures feed on gall-forming homopteran larvae.—Neotropical parrots eat mainly fruits and seeds (Forshaw 1989, Sick 1993), although there are some instances of insects and mollusc predation (Moojen et al. 1941, Roth 1984, Forshaw 1989, Sazima 1989). In March 1991, in lowland forest at Ilha do Cardoso State Park (25°03′05″S, 47°53′48″W; site description in Barros et al. 1991), I found a group of seven Maroon-bellied Conures (*Pyrrhura frontalis*) on the canopy of a 12-m-tall massaranduba tree (*Persea pyrifolia,* Lauraceae). The birds' bills were stained with a milky substance. They were eating one-cm-diameter galls that covered most of the leaves. The conures took the galls that grew along the margins of the leaves or took the entire leaf. The galls were held with one foot and opened with the bill. I could clearly see the conures picking white larvae from each gall, discarding the latter, macerating the larvae in their bills, and then swallowing them. The tree was fruiting, but the birds ignored the fruits completely. They continued to feed on the gall's larvae for 30 min. After they departed, I examined the ground under the tree and found it littered with opened galls, pieces of leaves, and a few unscarred fruits. Galls collected from the tree contained larvae that belonged to an homopteran. Two years later, during the first two weeks of March 1993, I made daily visits to the same tree. Maroon-bellied Conures were feeding on the gall's larvae every day. The galls, when young and small, were green like the leaf. Upon reaching their maximum size they became rusty-red. The conures took only mature galls, which contained the largest larvae.

Persea pyrifolia and other Lauraceae are known to be commonly infected by galls containing insects (J. Baitelo, pers. comm.). The tree's specific name was given due to the red color they get when infested by galls (F. de Barros, pers. comm.). Such infestations occur yearly and are a predictable resource for a gall-feeding animal.

There is a parallel between eating larvae in galls and eating seeds in fruits, and both food resources require the same mechanisms for locating and processing. It is well known that parrots know the precise location and timing of a food source and will use it year after year at the same season (Sick 1993). This probably applies to my observations during 1991 and 1993. Although the published information on eating of animal species by Neotropical parrots is scarce, such behavior may be more common and widespread than thought. Forshaw (1989) indicates that parrots are far more insectivorous than is generally suspected. Moojen et al. (1941) found 30 larvae of Diptera (Cecidomyiidae) in the stomach contents of two Bronze-winged Conures (*P. devillei*), and although this was considered a case of accidental ingestion, that seems unlikely. Schubart et al. (1965) found moth and Diptera larvae in the stomach of a Peach-fronted Parakeet (*Aratinga aurea*) and that 13 Diptera larvae were eaten by a Santarem Conure (*P. picta amazonum*). Captive Brazilian parrots are known to eat mealworms and meat, especially while breeding and as youngsters (Sick 1993; N. Kawall, pers. comm.). I believe that most instances of "accidental ingestion" of animal prey by parrots, in fact, represents intentional feeding of such items.

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Redirected copulation by male Boat-tailed Grackles.—Animals may direct activities toward an object or animal other than the usual releaser for the behavior (="redirection", Moynihan 1955), even though such a releaser may be available, at least in part (Ficken 1977). Redirected aggressive behavior has been reported frequently, but instances of redirection involving sexual tendencies are rare, usually involving captives (Ficken and Dilger 1960).

During observation periods totalling about 600 h in the breeding seasons of 1988–1993, I recorded four incidents of male Boat-tailed Grackles (*Quiscalus major*) copulating with objects other than female grackles. At Magnolia Gardens, South Carolina, on 15 June 1988, at 09:30 h EST, an unmarked adult (after second year) grackle copulated with a clump of dirt. The copulatory posture resembled that normally given by male Boat-tailed Grackles copulating with females: beak pointed down, wings spread and quivered, tail spread, plumage fluffed. The clump was roughly circular (ca 8 cm diameter). Between mounts, the grackle walked around the clump and assumed the cock-posture (Selander and Giller 1961). The male mounted the clump at least five times, but had difficulty in maintaining an upright position on the clump, because it rolled.

At Magnolia Gardens on 23 May 1991, at 08:19, a color-banded adult (3-yr-old) male copulated with a magnolia (*Magnolia grandiflora*) flower in the outer subcanopy of the tree, at about 15 m. The bird made ventral contact with the underside of the flower, which was made possible by the flower's slightly inverted position on its stem. After dismounting, he left the tree, but returned 8 min later. He landed next to the same flower, sang, and again copulated with it for 2 sec. He then flew from the tree, and was intercepted (supplanted in flight; Post 1992) by a marked adult (≥5-yr) male above him in the local dominance hierarchy. The dominant bird then landed directly on the same flower, and copulated with it for 3 sec, dismounted, sang, and then left the tree. He returned 29 min later and again landed directly on the same flower, copulated 3–4 sec, and then left to join a nearby group of feeding males.

On Sullivan's Island, South Carolina, on 21 June 1993 at 10:00, an unbanded second-year male grackle attempted to copulate with a faded green tennis ball (diameter, 6.4 cm). Although the bird appeared to have his vent in contact with the ball, he was unable to

maintain his position for more than 1 sec because the ball rolled each time he mounted it. The grackle attempted copulation at least six times in 3 min. The bird did not vocalize. No other grackles were in view.

These instances of redirected copulation are similar to those described for other species in the wild. Simon (1940) reported that male Sage Grouse (*Centrocercus urophasianus*) frequently tread clods of earth. Young (1949) reported a case in which a male American Robin (*Turdus migratorius*) attempted to copulate with a dirt clump, after being repulsed in soliciting a female. In these cases, and those described for captive birds (Ficken and Dilger 1960), a common element is the presence of an appropriate sexual stimulus, but a thwarting of the sexual drive. Within a given area, many male Boat-tailed Grackles solicit females, but usually only a few high-ranking males actually copulate (Post 1992). Similarly, in the lek-breeding Sage Grouse, only a few males do most of the breeding (Wiley 1973). It is possible that redirected copulation such as described for Sage Grouse and Boat-tailed Grackles may be related to the limited mating opportunities of males.

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ORNITHOLOGICAL LITERATURE

GREAT AUK ISLANDS. A FIELD BIOLOGIST IN THE ARCTIC. By Tim Birkhead. T & A D Poyser, London. 1993: 275 pp., 1 color illustration, 36 black-and-white illustrations, 13 color photos, 25 numbered text figs, including easily interpreted maps, $22.—The title "Great Auk Islands" suggests that the British author's latest book is largely a history of the Great Auks which were depleted to extinction by humans in the past century. The reader soon discovers that, of the book's nine chapters, only one is devoted largely to Great Auks, simply because so very little was recorded on the species' life history, not only at sea, but also at its breeding colonies where slaughtering was wholesale. Many of our seafaring forbearers must have visited the breeding sites, but apparently none among them was curious enough to observe and record the habits of these birds. Not recorded were even the most rudimentary observations on egg-laying times and chick-rearing periods, although one hopes that undiscovered notes on the species will surface some day.

Tim Birkhead left no stone unturned in scrutinizing the literature on Great Auks. His findings, disappointing for lack of factual material, nevertheless capsulize nicely relevant records for the species, including accounts of its heartrending demise. But the main thrust, indeed the soul of the text, is about his scientific studies on the Great Auk's closest extant relatives, especially his beloved Common Murre (*Uria aalge*), called Common Guillemot by Britons. He studied these murres in several localities, but the setting in this book is on a cluster of little-visited "Gannet Islands" off the coast of Labrador, although no Gannets occupy them. After reading, and frequently rereading his findings, I am convinced that few wild birds are better suited to resolving certain biological enigmas. I was astounded to learn that the density of breeding Common Murres on flat terrain far exceeded anything I had witnessed, even among closely nesting penguins. Not in sheer numbers that may reach a million or more at some penguin colonies, but in closeness of incubating birds. An exception is the male Emperor Penguin (*Aptenodytes forsteri*) that holds a single egg on his feet while huddling close together with his neighbors during the frigid Antarctic winter. One of Birkhead's mind-boggling photos (p. 103) shows 76 murre eggs within a single square meter quadrate: the social implication of such densely packed incubating individuals is biologically intriguing. These are the sorts of problems that Birkhead tackles head-on, and about which he later relates his findings in a manner understandable to biologists and non-biologists alike.

Among many captivating topics presented by the author, one that stimulated my curiosity dealt with the shape of the murre's egg which is noted for its extremely pointed little end. Its shape supposedly allows it to spin like a top, rather than roll off a cliff ledge—hence the oft-quoted belief that the evolved shape is adapted to a narrow cliff ledge. Birkhead says one merely has to watch a murre accidently knock its egg and watch it roll into evolutionary oblivion, to realize that the spinning top theory is nonsense. Alas, many of us have perpetuated the myth, hopefully, no longer. This revelation is incentive enough to climb to a murre colony and from a blind experience firsthand these special birds and their eggs.

Conceivably the oddly shaped egg may be adapted to the unusual upright incubating position of the murres with their single central brood patch (fig. 9, p. 93). Razorbills (*Alca torda*), with a rounded egg and lateral brood patches, have a prone incubating posture. Birkhead speculates that the Great Auk, with its pointed egg and single central brood patch, also had an upright incubation posture. One can expand this hypothesis: Emperor Penguins (also the closely related King Penguins, [*Aptenodytes patagonicus*]) incubate upright and have pointed eggs dissimilar to those of other penguin species with prone incubation pos-

tures. Also, like the murres, but unlike most seabirds, the two penguins show alloparental behavior (caring for neighboring chicks), evidently a biological advantage in super densely crowded conditions.

One concludes from this study that murre biology must be among the best documented by field ornithologists to date. Tim Birkhead takes his murre study a step further by reconstructing the life history of the Great Auks through his extensive knowledge of the murres. The result is pure speculation but nonetheless is convincing and is likely to prove out should further records come to light. His clever reconstruction was the highlight of the book for me.

Non-biologists wishing to learn more about scientific methods used by field biologists would do well to read this book. In a delightful manner that most anyone can comprehend, Tim Birkhead introduces biological concepts rarely mentioned outside of scientific journals, e.g., breeding synchrony, egg and chick recognition, kin selection, sperm competition, ecological segregation, and DNA fingerprinting, often crediting pioneer studies to their authors. Considerable parts of the text with accompanying photo illustrations clarify logistical and personnel problems that are often encountered on field expeditions: old hat stuff to experienced field biologists, but probably useful and interesting to the inexperienced. The final chapter entitled "Changes" will fascinate all readers. Following an interval of nine years, Birkhead revisited the Gannet Islands only to find many of its bird colonies devastated by arctic foxes (*Alopex lagopus*). He, as with so many others in similar situations, was faced with an all too frequent dilemma. Should one eradicate the foxes to protect the bird colonies, or does one let nature take its course inasmuch as the foxes were not introduced by humans? No easy solution here.

The text is packed full of art illustrations from start to finish. All 36 black-and-white illustrations by David Quinn are superb and enhance the book immensely. The one of a puffin chick in its burrow (p. 72) is a masterpiece, a technique I found especially difficult to master in trying to illustrate petrels deep within nesting burrows.

The book has a few minor flaws. However, no fault of the author, who includes even the lists of local names of Labrador birds. The continuing problem of deciphering common bird names on both sides of the Atlantic is simply maddening, especially with seabirds. Interpreting what species is a murre or guillemot often becomes more troublesome than the meaningful description of the species itself. For ornithology's sake, Europe and North America should resolve this problem once and for all by agreeing on the common names of birds.

Perhaps, because I came from a United Kingdom ancestry, I am chagrined by Birkhead's insensitive remarks concerning North American women: "The female member—one of those frighteningly aggressive, no-nonsense sort of North American ladies that one occasionally encounters." I interpret this remark to be sexist and above all non-scientific. I also note that he exalts the British Royal Air Force while downgrading the U.S. Air Force. Strange that a first-rate scientist, who almost certainly can command an extraordinary North American audience, would engage in such unprofessional behavior. Other than these puzzling inclusions, I strongly recommend the book for the biologist and non-biologist alike.—David F. Parmelee.

Noms Français des Oiseaux du Monde. (French Names of Birds of the World). By Commission internationale des noms français des oiseaux. Éditions Multimonde Inc., 930 Pouliot, Sainte-Foy, Québec, Canada G1V 3N9. 1993: 452 pp. $39.95 CDN.—Under the co-presidentship of Pierre Devillers and Henri Ouellet, this volume is the first of its kind by an international commission on vernacular names and sets precedents to be followed in other languages, especially in English, where some cleanup of names is needed at the international level. Between 1976 and 1980, Devillers published a series of articles in *Le*

international level. Between 1976 and 1980, Devillers published a series of articles in *Le Gerfaut,* a Belgian ornithological journal, featuring proposals and justifications for french names of the birds of the world. This endeavor started with the ostrich family but never got past the accentors (Prunellidae) after nine articles, covering some two-thirds of the species. International interest on bird names resurfaced during the International Ornithological Congress in Ottawa, in 1986. An international commission was set up for the next meeting in New Zealand. Several years later, Normand David, one of the commission's members, took it upon himself to finish the list of some 3000 bird names missing from Devillers's list, including most passerines.

The commission is to be applauded for establishing standards for a list of vernacular bird names. A major effort was put into applying them with scrutiny. The rules set forth here are based upon uniformity and brevity using a two-level system as in scientific nomenclature. The rules at the generic level were especially emphasised and included the following: (1) A generic name should apply only to a group of related species; at least, names should not suggest false relationships between non related species of different groups; (2) Some broad generics are to be preferred to odd ones for uniformity; (3) Similar species from remote areas should bear generics that reflect their parental relationships; (4) No single name should apply to any two or more different species; (5) A name chosen for a species should apply to all populations of that species; and (6) Well known names should not be modified unless they convey an error or are misleading at the international level.

An effort was made to shorten the length of names and to reduce the number of names with adjectives like "common", which still appears 178 times in the index for English names.

The taxonomic order follows Storer (Avian Biol. 1:1–18, 1971) for non-passerines and Sibley and Monroe (Distribution and Taxonomy of Birds of the World, Yale Univ. Press, 1990) for passerines. The book is divided into three parts. The main listing includes scientific names, followed by French names, and a reference number without systematic value, but useful for cross references with indexes. These names are followed by a separate repertoire of 18,500 English equivalents. The listing ends with indexes for French and scientific names. In some cases up to eight English, five French, and three scientific names used as synonyms are given in the indexes. The repertoire of English names is presented in alphabetical order of the complete name of the birds, to avoid complicated cross references of frequent three level names, and because of the lack of standards for either the presentation of such lists or for the use of hyphenation. Names in English follow regional spelling—e.g., gray and colored in American bird names, grey and coloured in other regions. When several species have the same name in English, all references to their scientific or French counterparts are given.

Synonyms are labeled as such in the index of the French and scientific names. As complementary information, a French name was given to subspecies in some instances, when deemed appropriate.

In French, the need for such a list originated from the large influx from Europe of books on birds including North American species, that often included inappropriate translations of names. With the growing number of international commissions and agencies at all levels of governments, this list was also considered important, especially for agencies dealing with biodiversity and conservation. Even bird watchers traveling abroad must know proper names for birds in other countries. Finding an Arctic Warbler (*Phylloscopus borealis*) in Alaska close to a Wilson's Warbler (*Wilsonia pusilla*) can be misleading, because they belong to completely different families.

Many names still in use in English would not fit some of the rules set forth in this book. There are several species bearing a shared name (White-throated Bulbul for five different

species from three different genera—*Phyllastrephus albigularis, Criniger chloronotus, Alophoixus flaveolus, A. bres, A. phaeocephalus,* Yellow White-eye for four species—*Zosterops senegalensis, Z. nigrorum, Z. luteus, Z. flavifrons,* Rufous Flycatcher for three species—*Myiarchus semirufus, Ficedula strophiata, Neocossyphus fraseri,* including two from different families, Robin—*Petroica australis, Erithacus rubecula,* and Rock-loving Cisticola—*Cisticola emini, C. aberrans* for two species each), names with confusing parental relationships (White-tailed Robin, *Cinclidium leucurum,* a Saxicolinae not closely related to *Turdus*), long many leveled names (Black-billed Blue-spotted Wood Dove, *Turtur abyssinicus*), lack of uniformity in hyphenation (Finsch's Rufous-bellied Fruit Pigeon, *Ducula finschii* but Snowy-cheeked Laughingthrush, *Garrulax sukatschewi*), some generics applying to non-related genera or species (Warblers and Sparrows), some qualifiers (common, western) that may not apply throughout the range of some species. For some birders, names are as awkward in English (Umboi Myzomela, *Myzomela cineracea*) as others are in French (Gérygone soufrée, *Gerygone sulphurea*), since about one third of the vernacular names are adaptations in French or English of their scientific names.

International French names for birds might not be accepted readily for every day use, as would be the case in English, and much work is still needed for a standard list of names of birds of the world in other languages. This book is a must for anyone working at the international level with bird names, especially translators, and not only for users of names of birds in French but also in English or Latin, because of the usefulness of the many synonyms to be found in the indexes in all three languages.—André Cyr.

Shorebirds of the Pacific Northwest. By Dennis Paulson, illus. by Jim Erckmann. Univ. of Washington Press, Seattle, Washington. 1993: xv + 406 pp., 98 color photographs, 52 numbered text figures, 36 tables, 10 distribution maps, 5 appendices. $40.00.—The author states that this book is intended to be a "fact book" that supplements field guides. Indeed, this book provides such a wealth of facts that it will be valuable anywhere in North America.

For this book, the Pacific Northwest is approximately a square covering Oregon, Washington, Idaho, western Montana, and southern British Columbia. All 62 shorebird species with at least one solid record in this region are given full treatment. Sixteen others receive lesser treatment because they might be found as vagrants in the region. The combined 78 species is more than are included in the "National Geographic Society Field Guide to the Birds of North America, Second Edition" (1987)! Paulson's exhaustive coverage of nearly all North American shorebirds transcends the geographic limits of the book's title.

Nevertheless, the focus is regional. The treatment of seasonal, distributional, and habitat occurrence of each species is very detailed for the region, with between one and two pages per species. Bar graphs summarize the seasonal status of every species, separately for the coast and interior subregions. Maps indicate the breeding range in the region for ten species.

Introductory and general chapters occupy 82 pages, versus only 20 in the superb "Shorebirds: An Identification Guide to the Waders of the World" by Hayman, Marchant, and Prater (1986). Although the earlier book is essential for any shorebird observer in the world and its introductory pages are useful and concise, "Shorebirds of the Pacific Northwest" provides a superior understanding of shorebirds and how to learn them. Innumerable valuable tips on finding and identifying shorebirds are interwoven with lucid explanations of shorebird ecomorphology and plumage colors and their consequences for identification. Paulson employs a multifaceted analytical approach that categorizes shorebirds in turn by size, shape, flight patterns (wing, tail, rump), other field marks, and distributional/seasonal groups. Good figures illustrate feather color patterns, degrees of primary projection, and the

relative occurrence of plumages classes through the year. A glossary of basic terms (e.g., rectrices) would have helped beginners. Sections on the shorebird's year and identification problems are particularly helpful. Paulson's insightful discussion of "jizz" should be required reading for all, especially anyone that believes that components making up "jizz" are indefinable or that "jizz" can confirm (versus suggest) the identity of a bird.

Species account lengths up to ten pages suggest the depth of treatment. Sections that are self-explanatory include Distribution, Habitat and Behavior, Subspecies, Identification, In Flight, and Voice. "Northwest Status" combines detailed narrative and bar graphs. Paulson lists many data for high counts and extreme dates, separately for adults and juveniles when possible. Some records accepted in the text are not shown in the seasonal bar graph. "Structure" relates the species' physique to the illustrated definitions in the introductory chapters. This includes consistent, well-illustrated use of primary projection, a revealing new generation field mark. "Plumage" supplements good descriptions with a bar graph showing the normal seasonal occurrence of each plumage in the Pacific Northwest. Many "Further Questions" suggest needed systematic quantitative observations on behaviors and age-specific patterns. "Notes" often challenge published statements or records that Paulson believes dubious or erroneous. He lists the location of photos published elsewhere, and corrects misidentifications of species or plumage in the cited work. The listing of references for each species and the 23-page Literature Cited are especially commendable in the face of the distressing tendency of bird guide authors to cite few literature sources.

There are modern, thorough treatments of identification for such groups as golden-plovers, stints, and dowitchers. I found a few errors in distribution. Paulson states that the only interior California records of Pacific Golden-Plover (*Pluvialis fulva*) are from the Salton Sea; it occurs in the Central Valley as well. Paulson writes that the subspecies *griseus* of the Short-billed Dowitcher (*Limnodromus griseus*) breeds in "the Maritime Provinces" instead of Quebec, and that this species "normally winters no farther north than southern California;" in fact it winters abundantly around San Francisco Bay.

Paulson doesn't use the Humphrey and Parkes plumage terminology because it is "unfamiliar to most users of field guides." But his book, filled with so many facts that transcend field guides, was exactly the sort of book that could reverse this unfamiliarity. He also perpetuates the myth that "juvenal" is only an adjective (see Eisenmann 1965 Auk 82:105).

The captions of the 98 color photos integrate them well with the text and increase their value. The 226 color photos in "The Facts on File Field Guide to North Atlantic Shorebirds" by R. J. Chandler (1989) remain a more comprehensive and comparative photo reference, though Paulson suggests refinements on the plumage labeling of a few of Chandler's photos. The many drawings by Jim Erckmann effectively illustrate the desired points. Erckmann's close-ups and silhouettes are his best renderings; some of his flight views look stiff and flat on the page, lacking the perspective of Peter Hayman's in "Shorebirds."

This book was well designed and produced. Its index is superior to that in "Shorebirds." Appendices summarize for all species their seasonal status, extreme dates, weights and measurements, and include a gazetteer of cited localities.

"Shorebirds of the Pacific Northwest" provides an abundance of high quality information in verbal, quantitative, and pictorial forms. It deserves a place beside "Shorebirds" on every North American's bookshelf, and Pacific Northwest observers may keep it in their cars for frequent use.—Stephen F. Bailey.

The Peregrine Falcon. 2nd ed. By Derek Ratcliffe. Illus. by Donald Watson. Academic Press, Inc., San Diego, CA 92101, 1993: 454 pp., 4 color plates, 57 black-and-white pho-

tographs, numerous drawings, 22 numbered figs., 31 tables. $39.95.—This classic remains, in the second edition, the best single way to learn what peregrines (*Falco peregrinus*) are all about. Format remains mainly unchanged except that the excellent photographs are now placed to correspond with the text. The book is indispensable as a scientific reference and as a source of interesting general information. The need for a second edition relates mainly in the unprecedented increase of peregrines in the United Kingdom beyond pre-WWII levels. Britain and Ireland now have at least 1600 pairs, 142% of the pre-war estimate. Only the lowlands of southeastern England lack breeding pairs. The general increase, as elsewhere, follows the reduction of pesticide use, but the unexpected surge owes largely to pigeon racing, which supplies nearly half the food to breeding pairs in certain districts, and to the earlier decline in gamekeeping. Ratcliffe acknowledges the increase is not over. In several districts the density of pairs has increased because territory size has decreased, allowing pairs to use poorer crags. Clutch and brood size are also decreasing.

The book focuses on the British bird but includes a great amount of data from other populations. The sections on disease, population dynamics and the role of pesticides are rewritten from the first edition. Ratcliffe remains convinced, based on chronological evidence, that the cyclodiene organochlorines such as dieldrin were more important than DDT in population decline in the 1960s. The new analysis of reverse sexual size dimorphism concludes none of the various hypotheses has resulted in blinding revelation.

Despite the massive increase of peregrines in most parts of Britain, and widespread gains worldwide, Ratcliffe is concerned for this celebrated species. Locally in coastal Britain, oiling by Fulmars (*Fulmarus glacialis*) was found in 26% of a trapped sample of peregrines. Oiling is known to cause peregrine mortality and might contribute to the poor population recovery in northern Scottish coastal areas. Gamekeeping seems on the rise and could become significant. Pigeon fanciers are more and more adamant that peregrines in some areas be reduced. Ratcliffe believes the species is too entangled in human affairs to avoid impact by the further onslaughts on our natural environment that surely lie ahead.—James H. Enderson.

Wilson Bull., 106(4), 1994, pp. 778–788

PROCEEDINGS OF THE SEVENTY-FIFTH ANNUAL MEETING

JOHN L. ZIMMERMAN, SECRETARY

The Seventy-fifth Annual Meeting of the Wilson Ornithological Society was held Tuesday, 21 June through Sunday, 26 June 1994 at the University of Montana, Missoula, Montana in joint session with the American Ornithologists' Union and the Cooper Ornithological Society. The local committee, co-chaired by Richard L. Hutto and Donald A. Jenni, was composed of Gerry Baertsch, Joe Ball, Dona Boggs, Kenneth Dial, Erick Greene, Sallie Hejl, Del Kilgore, Jeff Marks, Tom Martin, Chris Paige, Alison Perkins, Roly Redmond, Sue Reel, Lynne Tennefoss, and Bret Tobalsake. The meeting was hosted by the Avian Studies Program of the Division of Biological Sciences at the University of Montana and the Five Valleys Audubon Society of Missoula.

The Council met from 08:10 to 15:30 on Tuesday, 21 June in room 304 Liberal Arts. On Tuesday registration for the approximately 1070 guests and members of all three societies was followed by an informal reception at Caras Park. The opening session on Wednesday convened in the Five Valleys Ballroom of the University Center at 08:30 with a welcome from the University of Montana and responses by Brina Kessel for the AOU, Lloyd Kiff for the Cooper Society, and Keith Bildstein for the Wilson Society.

Following a plenary address by Lewis Oring, University Nevada–Reno, entitled "Discovering avian mating systems: From Datwin to DNA," the 315 scientific papers were given from Wednesday through Saturday in concurrent sessions at various locations across the campus. Presenters of the 168 posters were available on Thursday and Friday evenings in conjunction with a social offering light refreshments at the University Center. Early morning field trips to local areas were conducted throughout the conference by members of the Five Valleys Audubon Society, while extended field trips on Sunday provided additional opportunities to sample the avifauna and general natural history of the area. A social hour preceded the annual banquet, which was held in the Five Valleys Ballroom of the University Center. After the banquet the following awards were presented:

EDWARDS PRIZE (for the best major article in volume 105 of *The Wilson Bulletin*)

Steven L. Lima for his paper, "Ecological and evolutionary perspectives on escape from predatory attack: A survey of North American birds." Wilson Bull.105(1):1–47.

ROGER TORY PETERSON INSTITUTE TRAVEL AWARDS

Paul R. Sievert, "Water balance constraints on the hatching success of tropical terns and sheanwaters."

Andrew W. Kratter, "Habitat selection in bamboo specialist birds."

ALEXANDER WILSON PRIZE (for best student paper)

William A. Schew, "Metabolic responses of European Starlings and Japanese Quail chicks to undernutrition: developmental constraint vs adaptive response."

FIRST BUSINESS MEETING

Since President Conner was unable to attend due to recent surgery, the first business meeting was called to order by Vice-president Bildstein about 20:00 on Wednesday, 22 June

in Room 115 of the Music Building in conjunction with the combined business meetings of all three societies. Secretary Zimmerman presented the report of the nominating committee (Mary Clench, chair, Robert Burns, Herbert Kale): President, Richard N. Conner; First Vice-president, Keith L. Bildstein; Second Vice-president, Edward H. Burtt, Jr.; Secretary, John L Zimmerman; Treasurer, Doris J. Watt; Members of the Council, 1995–1997, William E. (Ted) Davis, Jr. and Carol A Corbat. Secretary Zimmerman also read the suggested changes in the Bylaws and Constitution of the Wilson Ornithological Society as previously published in *The Wilson Bulletin*—to repeal Bylaw 7 which sets the fiscal year, to repeal item 5 of Bylaw 8 which deletes the election of members from the agenda for the annual meeting, and to amend Article II, section 2 of the Constitution to delete reference to the election of members so as to read "Any person who is in sympathy with the objectives of the Society may become a member by submitting an application and appropriate dues to the Treasurer."

The names of decreased members of all three societies were read by Secretary McDonald of the American Ornithologists' Union. Wilson Society members included in this list are Karl E. Bartel (Blue Island, IL), T. A. Beckett, III (John's Island, SC), William D. Dugan (Hamburg, NY), Joseph J. Hickey (Madison, WI), M. E. "Pete" Isleib (Juneau, AK), Theodore R. Miley (Ann Arbor, MI), Charles E. Nelson (Brookfield, WI), Theodore A. Parker, III (Washington, DC), Paul A. Stewart (Oxford, NC), and Joseph W. Tayler (Honeoye Falls, NY).

The following resolutions, jointly sponsored by all three societies, were presented by Martin G. Raphael, and all were passed by unanimous votes:

RESOLUTION IN SUPPORT OF VOLUNTEERS

WHEREAS, volunteers have made extraordinarily valuable contributions to the systematic collection of scientific information about birds since Spencer Baird marshalled a cadre of amateurs across the United States in the mid-1850s to collect data for the Smithsonian Institution on migration and breeding phenology; and

WHEREAS, the operation of many field and museum initiatives and current bird monitoring programs, such as the Breeding Bird Survey, waterfowl surveys, and bird banding operations in the North America continue to depend heavily upon volunteers, and

WHEREAS, the Breeding Bird Survey, the Bird Banding Laboratory, and the Biological Survey Program National Museum of Natural History) are currently administered under the National Biological Survey (NBS) In the Department of the Interior, and

WHEREAS, no comprehensive long-term policy for the use of volunteers for programs within the NBS has been formulated,

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, the Cooper Ornithological Society, and the Wilson Ornithological Society join with the Ornithological Council to petition the Secretary of the Interior and the Director of the NBS to work with Congress to promulgate language in authorizing legislation for the NBS to ensure that volunteers can be used on all NBS projects.

RESOLUTION IN SUPPORT OF BREEDING BIRD SURVEY

WHEREAS, the Breeding Bird Survey (BBS) is recognized as the most comprehensive, extensive, and useful monitoring program for nongame breeding bird species in the Western Hemisphere, and

WHEREAS, the results of analyses of the BBS data help to identify both bird species and their associated habitats that are at risk in the United States and elsewhere in North America, and

WHEREAS the BBS is now administered with the Inventory and Monitoring Program of the National Biological Survey (NBS), and

WHEREAS, support for the Survey has been reduced since the formation of the NBS and uncertainty exists concerning staffing,

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, the Cooper Ornithological Society, and the Wilson Ornithological Society join with the Ornithological Council to petition the Secretary of the Interior and the Director of NBS to ensure that the BBS be given sufficient staff and funding to permit a sustained coordination of BBS programs and to enhance the analytical capability for determining the status and trends of nongame bird populations.

RESOLUTION IN SUPPORT OF PIPING PLOVER

WHEREAS the prairie population of the Piping Plover (*Charadrius melodus*) has been classified as Endangered by the Committee On the Status of Endangered Wildlife In Canada (Canada) since 1985, and declared Threatened by the United States Fish and Wildlife Service since 1986, and

WHEREAS the population of the Piping Plover has been declining steadily since the early 1970s, and

WHEREAS in some years 5% of the breeding population use Lake Diefenbaker, in Central Saskatchewan for breeding, and

WHEREAS in some years, the population at Lake Diefenbaker is the largest single population of this species in the world, and

WHEREAS in some years the raising of lake levels by the Saskatchewan Water Corporation on Lake Diefenbaker results in a significant loss of annual productivity of this species,

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, the Cooper Ornithological Society, and the Wilson Ornithological Society strongly recommend that the Saskatchewan Water Corporation reexamine their schedule of filling Lake Diefenbaker, so that losses of Piping Plover eggs and/or chicks are minimized.

RESOLUTION IN SUPPORT OF HABITAT PROVISIONS OF THE ENDANGERED SPECIES ACT

WHEREAS the Endangered Species Act is one of the most important and fundamental laws for biological conservation, and

WHEREAS the Endangered Species Act makes it unlawful to "harm" an endangered species, and

WHEREAS no species can exist in nature without its habitat, and

WHEREAS the potential for a species to continue to exist in nature is directly related to the quality of its habitat, and

WHEREAS it therefore follows that any significant degradation or loss of habitat necessarily must harm an endangered species, and that any attempt to conserve an endangered species necessarily must include conservation of its habitat, and

WHEREAS a recent District of Columbia Circuit Court of Appeals decision (Sweethome vs Babbitt, 1994) found that the definition of "harm" under the Endangered Species Act could not include a prohibition against habitat destruction or modification;

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, the Cooper Ornithological Society, and the Wilson Ornithological Society find that the Sweethome decision is contrary to scientific understanding and that no law that purports to protect endangered species can do so effectively without protecting their habitat.

BE IT FURTHER RESOLVED that if the Sweethome decision is upheld in the courts,

The American Ornithologists' Union, The Cooper Ornithological Society, and The Wilson Ornithological Society urge Congress to clarify that inclusion of habitat destruction or alteration is an explicit component of "harm" under the Endangered Species Act.

CONSERVATION OF BIODIVERSITY IN CUBA

WHEREAS the Caribbean is a priority region in the Western Hemisphere for the conservation of tropical biodiversity, and

WHEREAS Cuba is the largest country in the Caribbean and is considered to be a unique biogeographical province, with the greatest number of flowering plants and vertebrate species as well as the greatest number of endemic species in the West Indies, and

WHEREAS Cuba has the largest expanses of wetlands and some of the most biologically diverse coral reef and coastal ecosystems in the Antillean region, and

WHEREAS Cuba is one of the most important countries in Latin America for the conservation of migratory birds that breed in the eastern United States and Canada, and

WHEREAS many Cuba species and ecosystems are endangered due to changing land uses, and

WHEREAS Cuba has taken important steps toward establishing a national network of protected areas to preserve the biological diversity of the region, and has achieved one of the lowest human population growth rates in Latin America, and

WHEREAS the present restrictions imposed by the U.S. government impede for bilateral cooperation in conservation programs, and

WHEREAS the United States is signatory to various international agreements for the conservation of biodiversity and migratory species in the Western Hemisphere,

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, the Cooper Ornithological Society, and the Wilson Ornithological Society urge the President and Congress of the United States to:

1. Promote United States–Cuba–Canada trilateral meetings of scientists and conservationists to discuss common concerns and priorities pertaining to biological conservation in eastern North America and the Caribbean region.
2. Promote academic and scientific exchange programs among government agencies and universities in the United States and Cuba.
3. Provide financial support towards the conservation of natural protected areas in Cuba, especially those known for their importance to the preservation of regional biodiversity, endemic, and migratory species.
4. Eliminate all restrictions that prevent members of non-governmental organizations, charitable foundations, and academic institutions from travelling to Cuba and supporting research, education, and conservation projects.

SUPPORT FOR THE FISH AND WILDLIFE CONSERVATION ACT OF 1980

WHEREAS, fish and wildlife in the United States are of ecological, educational, aesthetic, cultural, recreational, economic, and scientific value, and represent a valuable national public resource, and

WHEREAS, more than 75 million Americans enjoy viewing, photographing, and studying wildlife, and

WHEREAS, expenditures on viewing, photographing, and studying wildlife in the United States exceed $18 billion annually, and

WHEREAS, a pressing need exists for the management and enhancement of nongame wildlife species, and

WHEREAS, there has never been an adequate source of federal monies to fund programs for nongame wildlife, and

WHEREAS, a highly successful funding mechanism, the 1937 Federal Aid in Wildlife Restoration Act (Pittman-Robertson), provided reliable funding for the research and management of game species, and

WHEREAS, the United States Congress recognized the need for a more comprehensive wildlife management program through passage of the 1980 Fish and Wildlife Conservation Act, reauthorized in 1986, 1990, and 1992, and

WHEREAS, no funding for the Act has ever been requested by the Executive Branch, nor appropriated by Congress, and

WHEREAS the funding ceiling for the Act of $5 million is far below the estimated $100 million needed, and

WHEREAS many state agencies have already attempted to implement the Act with limited state funding, but need federal support, and

WHEREAS, adequate funding for the Act could be far less expensive than costly endangered species restorations,

THEREFORE BE IT RESOLVED that The American Ornithologists' Union, The Cooper Ornithological Society, and The Wilson Ornithological Society endorse the implementation of a tax on nongame, bird-related activities and/or supplies to generate funding for this Act.

SUPPORT FOR THE NATIONAL INSTITUTE FOR THE ENVIRONMENT

WHEREAS, the health of the environment must be regarded as seriously as human health, and

WHEREAS, a solid scientific basis is essential for effective programs to protect the environment, and

WHEREAS, there is a need in the United States for a coordinated national program to support fundamental and applied environmental research and training encompassing a wide variety of disciplines aimed at understanding, preventing, and solving environmental problems, and

WHEREAS, such research and training is presently uncoordinated and largely underfunded, and

WHEREAS, a consensus is emerging in the scientific community that a government agency that supports mission-oriented competitively-awarded research, may be the most appropriate vehicle to encourage, promote and support environmental research and training, and

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, the Cooper Ornithological Society, and the Wilson Ornithological Society support the proposal for the National Institute for the Environment (NIE) and encourages Congress and the Administration to create the NIE.

COMMENDATION

WHEREAS the American Ornithologists' Union, the Cooper Ornithological Society, and the Wilson Ornithological Society held their first joint meeting in Missoula, Montana on the campus of the University of Montana, at the invitation of the Avian Studies Program, Division of Biological Sciences, University of Montana, and the Five Valleys Audubon Society, Missoula, and

RECOGNIZING that the Committee on Local Arrangements, under the outstanding direction of Richard L. Hutto and Donald A. Jenni, provided us with an exceptionally diverse assemblage of exhibits, special events, field trips, and evening social events, and

RECOGNIZING that the Committee on the Scientific Program under the equally capable

direction of Edward H. Burtt, Jr., arranged outstanding scientific lecture sessions, workshops, and poster sessions, and

RECOGNIZING that James A. Kushlan performed an outstanding service in coordinating the Scientific Program among the three societies, and

WHEREAS all those who have attended this meeting have been enriched by it,

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, the Cooper Ornithological Society, and the Wilson Ornithological Society commend the Committee on Local Arrangements and the Committee on the Scientific Program for their efforts toward this historic meeting.

SECOND BUSINESS MEETING

The second business meeting was called to order by Vice-president Bildstein at 13:03 on Friday, 24 June, in Liberal Arts 305. Ruth Beck in colonial dress offered a dramatic invitation to attend the Williamsburg, VA meeting 4 to 7 May 1995. In addition to our regular business and scientific sessions there will be opportunities for daily and specialty field trips to a variety of habitats, including offshore islands. There will also be a full schedule for families and spouses to historic areas and other attractions.

Secretary Zimmerman then presented the following summary of the Council meeting. Our present membership is 2451, representing an overall 8% increase over last. Of particular interest is a 21% increase in student members. We attribute the healthy state of our membership to the efforts of the membership committee, chaired by John Smallwood. The Undergraduate Outreach Committee, chaired by Ernie Willoughby, is continuing to analyze the 200 questionnaires on undergraduate offerings in ornithology that were returned in last year's survey. One expressed need by responders was for greater communication of information of interest to undergraduates, for example, summer job opportunities and internships in ornithology. The committee is actively pursuing the development of an electronic bulletin board to satisfy this need. Charles Blem was unanimously elected to serve another one year term as editor of *The Wilson Bulletin.* The Council decided to continue our support of the Ornithological Council by an annual contribution of $500 for the next two fiscal years. The Council also reaffirmed our desire to award the Edwards Prize to the best paper published in the past volume of *The Wilson Bulletin.* Invitations for future meetings have been received and accepted for Cape May, NJ, 11–14 April 1995 and Manhattan, Kansas in April, 1997. Greensboro, NC is contemplated as the meeting locale in 1998.

Doris Watt presented the treasurer's report.

The fiscal year ending 31 December 1993 was a good year for the Wilson Ornithological Society. With total receipts of $112,800.04 and total disbursements of $97,343.27, the society was ahead by $15,456.77 at year's end. Total cash on hand was $102,469.16 and the endowment market value was at $487,786 making total assets for the society $590,255, up from last year's $551,270.

As recommended by the council last year, the Nice, Wilson and Fuertes awards were set at $200, $200 and $600, respectively. The two designated accounts (Stewart and Sutton) were evaluated and assigned a proportion of the endowment principal. This year these accounts provided sufficient income in spite of a low income interest rate. As recommended by the council, the Edwards Prize has been suspended as a cash award until the endowment plans are determined. Its endowment principal is now approximately $1600.00.

As we change the society's fiscal year to July 1 through June 30, I will be filing a half-year report with the IRS (Jan–June 1994), as well as a regular yearly report. The 1994 budget was approved at last year's meeting, but this year we will be looking at a budget

for July 1994–June 1995. I have re-calculated estimates to bring them more in line with recent increases in both income and expenses.

REPORT OF THE TREASURER
1 January 1993 to 31 December 1993

GENERAL FUNDS

Balance Forward		$121,012.39
Receipts		
Regular and sustaining memberships	$ 33,840.00	
Student memberships	4,476.00	
Family memberships	176.00	
Total dues		$ 38,492.00
Subscriptions for 1992	$ 25,560.86	
Back issues	468.00	
Contributions from authors for page charges	19,300.48	
Newsletter subscriptions	80.30	
Total income from the Bulletin		$ 45,409.64
Contributions to The Van Tyne Library	$ 268.00	
Contributions to the Sutton Fund	100.00	
Contributions to the Roger Tory Peterson Fund	1,000.00	
Contributions to the General Endowment	674.00	
Contributions to General Endowment (Life Patrons)	3,250.00	
Unrestricted contributions	249.00	
Total contributions		$ 5,541.00
Royalties and List rental	2,841.45	
Interest from Endowments and Bank account	18,827.36	
Dividends from Dreyfus account	1,558.09	
Miscellaneous	130.50	
TOTAL RECEIPTS		$112,800.04
Disbursements		
Bulletin Publication		
December 1992	$ 21,419.02	
March 1993	18,896.89	
June 1993	16,162.19	
September 1993	14,870.80	
Editor's expenses	5,348.89	
Total publication costs		$ 76,697.79
OSNA expenses	$ 14,181.00	
Secretary's expenses	57.46	
Treasurer's expenses	360.00	
Treasurer's bond	105.00	
Joint meeting planning costs	479.34	
Editor's travel expenses	320.00	
Incorporation fee	5.00	
Membership committee printing	135.50	
Postage and telephone	412.00	
Advertisement (Allen Press)	425.00	

Back issue storage	78.60	
Van Tyne Library	82.58	
Miscellaneous	4.00	
Total operating expenses		$ 16,645.48
Organizational Awards	$ 3,500.00	
Ornithological Council	500.00	
Total Philanthropies		$ 4,000.00
TOTAL DISBURSEMENTS		$ 97,343.27
Transfer to Endowment		$ 34,000.00
Total Debits		$131,343.27
Ending Balance		$102,469.16

CASH ACCOUNTS

First Source Bank checking account 31 December 1993	$ 45,680.70	
Editor's Account Balance 31 December 1993	$ 4,900.54	
Dreyfus liquid assets 31 December 1992	51,887.92	
Total cash on hand		$102,469.16

TOTAL ENDOWMENT FUNDS

1993 Market Value	$487,786.00

The editor's report was submitted by Charles Blem as follows:

EDITOR'S REPORT—1993

In 1993, 185 manuscripts (105 major papers, 80 short communications) were received by *The Wilson Bulletin* editorial office. This is 5 more than in 1992. Of these, 42% were accepted and 58% were rejected. The time between receipt of manuscript from the author(s) and our return of the manuscript with referee comments nearly always has been less than three months. No manuscript required more than four months for a decision. There is a small backlog of manuscripts, but accepted revisions almost always have been published in the next scheduled issue. Frontispiece articles take a bit longer. The average time between receipt of a manuscript and its appearance in *The Wilson Bulletin* in 1993 was almost always less than a year. A few papers required longer because authors were slow to return revisions.

I am grateful to the editorial board—Kathy G. Beal, R. N. Conner, J. A. Smallwood, C. R. Smith and C. H. Stinson—for their timely, skilled evaluations of many of the manuscripts submitted to the journal. I also thank George A. Hall for his editorship of the book reviews section. Assistant Editors Leann Blem, Albert E. Conway, and Karen Killeen are responsible for the consistency of style and format, and for making arcane prose more readable. I thank them for their efforts. Kathy G. Beal deserves special praise for continuing to assemble the index for *The Wilson Bulletin*. This is a tedious task and the entire society benefits from her careful work. For six years Leann Blem has provided much of the manual labor that keeps the editorial office running and she catches many of the small errors that can plague a publication. As always, I remain open to suggestions as to how to improve the service we provide the readers and authors, and invite you to make your opinions known to me.

C. R. Blem, *Editor*

Charles R. Smith presented the report of the Auditing Committee: On 24 June 1944, the Audit Committee, consisting of Paul J. DuBowy and Charles R. Smith, reviewed the financial statements of the Wilson Ornithological Society for the period 1 January through 31 December 1993. We find the financial statements of the Society to be in good order and to be reported in a clear, concise, and detailed manner. We commend the Treasurer, Doris J. Watt, and our investment advisor, Phillips Street, for their responsible stewardship of the finances of the Society.

Judy McIntyre, chair of the research committee, announced the following awards:

LOUIS AGASSIZ FUERTES AWARD

Diane Neudorf, "Female control of extra-pair fertilizations: fertility advertisement in Hooded Warblers."

MARGARET MORSE NICE AWARD

Paul A. Bedell, "Late-summer breeding of Sedge Wrens in the Great Plains."

PAUL A. STEWART AWARDS

Rita R. Colwell, "Female-biased sex ratios in spring migration of Rufous Hummingbirds at a banding site in central California."

Bonnie E. Stout, "Weather and fall migration of the Red-necked Grebe."

Camille Ward, "Economic decision-making in the American Crow (*Corvus brachyrhynchos*): How crows balance foraging considerations and predator avoidance in an urban environment."

Kristin Williamson, "Natal philopatry in Leach's Storm-petrels on Matinicus Rock, ME."

Aaron E. White, "Nest site microhabitat of the Spotted Owl in north-central California."

Vice-president Bildstein recalled the report of the nominating committee to the floor of the assembly. Chan Robbins moved and Herb Hendrickson seconded that the nominations be closed. The motion passed and Judy McIntyre then moved, with a second by Herb Hendrickson, that a unanimous ballot be cast for the nominated set of officers. The motion passed and a unanimous ballot was recorded.

Vice-president Bildstein offered the two changes in the Bylaws and the one amendment to the Constitution, as previously published for consideration. George Hall moved and Mary Clench seconded the motion to accept these changes, and the motion was passed. George Hall moved that the meeting be adjourned, seconded by Doris Watt, and it was accomplished at 13:30.

The reports of the standing committees are as follows.

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE—1993

The calendar years roll by faster and faster—as we get older this becomes increasingly evident. At annual report time, I try not to think solely (or even primarily) of the statistics, and of comparing them with those of past years. Some figures, as seen in this instance, fluctuate considerably, some downward but some upward. The important thing to a facility like our Society's library is to see that operations are running smoothly, with the procedures constantly enhanced and refined. There is a very great deal involved: the acquisition and storage of materials, proper supervision of their use, all the receiving and shipping, appropriate sales (of duplicate materials) and purchases (of useful new items), and copying, along

with all the related correspondence, cataloging, filing, handling of funds, and general keeping of records.

Endless thanks are due to paragon Janet Hinshaw, of the UMMZ Bird Division and our key person in charge of library activities, to those others who provide her with constant clerical persistence (especially Pat Ahrens), and to those of our membership at large, and others, who have given support in diverse ways, both by contributing and by using. To enlist even more such support as the years pass should remain our top priority.

Donations came from 16 members and institutions: R. Bayer, A. J. Berger, C. Collins, R. N. Conner, Ducks Unlimited, G. Hall (review copies), K. Haller, J. Hinshaw, H. Kolb, R. B. Payne, Point Reyes Bird Observatory, W. Post, J. Spendelow, P. Stettenheim, D. E. Varland, F. H. Wadsworth. These included 58 reprints (29), 15 books and monographs (4), 227 journal issues (103), 9 reports (6), and 1 dissertation. The numbers in parentheses are items received from A. J. Berger, who continues to be one of our staunch supporters—Thanks again Andy!

Exchanges from 125 institutions provided us with 164 journals, books, and related items. From 26 institutions we received 365 journals as gifts, and 19 were received as subscriptions from 13 organizations.

In all, 55 loans were made to 37 members and libraries of 16 books, 13 journals, 12 reprints, and 185 photocopied journal articles. We would like to increase the number of loans substantially; after all, this is what the library is for, in large part.

This year, $1702.50 was taken in for our library's new book fund from the sale of 67 books and 273 journal issues (all duplicates). Many of the sales were made at the annual meeting.

From our fund, 29 books, reports, etc. were purchased at a total cost of $812.86.

A total of 205 journal issues were donated by us to the Yale Peabody Museum and to the Biological Institute in Poland.

So we continue to thrive, and to a modest extent, prosper.

William A. Lunk, *Chair*

REPORT OF THE CONSERVATION COMMITTEE

The Conservation committee, composed of Jerome A. Jackson, chair, Craig Rudoph, Robert Hole, Stan Senner, and Grant Stevenson, has pursued the need to develop reports on predator control and the issuing of depredation permits by federal agencies, the bird markets of Indonesia and the importation of live birds from that country, and the current status of raptor management in North America.

Jerome A. Jackson, *Chair*

REPORT OF THE MEMBERSHIP COMMITTEE

The membership committee has a new member, David Cimprich, a doctoral candidate at the University of Southern Mississippi. The other three members are James Ingold at Louisiana State University, Mark Woodrey at the Mississippi Museum of Natural Science, and myself at the University of Florida.

The WOS membership poster was displayed at the WOS meeting in Guelph, Ontario, in April/May, and also at the RRF meeting in Charlotte, North Carolina, in November. Membership brochures were made available by the poster, and approximately three dozen were picked up at each meeting. David Cimprich has agreed to undertake the responsibility for arranging to have the poster displayed at national and regional meetings of interest to po-

tential WOS members. We look forward to a more aggressive travelling schedule for the membership poster.

During the past year I received 16 inquiries from people interested in joining our society. To each I sent a written reply, including information on joining the WOS (where to send the application, student membership rates, etc.) and a membership brochure. Mark Woodrey is sending membership invitations to authors who publish in *The Wilson Bulletin,* and Jim Ingold is contacting nonmembers who present papers or posters at the annual meetings, excluding those who receive complementary memberships.

Our supply of brochures is down to about 250, so we need to print some more in the near future. This would be an appropriate time to make any revision that may be desirable. Suggestions from the WOS council would be appreciated.

John A. Smallwood, *Chair*

The list of papers and posters presented at the meeting as well as the list of members and guests in attendance will be published as a supplement to volume 112 (1995) of *The Auk.*

Wilson Bull., 106(4), 1994, pp. 789–811

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BY KATHLEEN G. BEAL

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